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ANNALS OF THE
SOUTH AFRICAN MUSEUM

ANNALE VAN DIE
SUID-AFRIKAANSE MUSEUM

VOLUME 97

BAND 97



ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

VOLUME 97 BAND



THE TRUSTEES OF THE
SOUTH AFRICAN MUSEUM
CAPE TOWN

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SUID-AFRIKAANSE MUSEUM
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LIST OF CONTENTS

	Page
COOKE, H. B. S. <i>see</i> HENDEY, Q. B.	
HAARHOFF, P. J.	
A new fossil stork (Aves, Ciconiidae) from the Late Tertiary of Langebaanweg, South Africa. (Published January 1988.)	297
HENDEY, Q. B. & COOKE, H. B. S.	
<i>Kolpochoerus paiceae</i> (Mammalia, Suidae) from Skurwerug, near Saldanha, South Africa, and its palaeoenvironmental implications. (Published December 1985.)	9
HILLER, N.	
The South African Museum's <i>Meiring Naude</i> cruises. Part 16. Brachiopoda from the 1975-1979 cruises. (Published June 1986.)	97
HULLEY, P. A.	
A taxonomic review of the lanternfish genus <i>Triphoturus</i> Frazer-Brunner, 1949 (Myctophidae, Osteichthyes). (Published May 1986.)	71
HULLEY, P. A.	
Lanternfishes of the southern Benguela region. Part 1. Faunal complexity and distribution. (Published August 1986.)	227
KENSLEY, B.	
The fossil occurrence in southern Africa of the South American intertidal mollusc <i>Concholepas concholepas</i> . (Published October 1985.)	1
KENSLEY, B. & PETHER, J.	
Late Tertiary and Early Quaternary fossil Mollusca of the Hondeklip area, Cape Province, South Africa. (Published August 1986.)	141
LYONS, J. <i>see</i> MYERS, A. A.	
MYERS, A. A. & LYONS, J.	
A re-evaluation of the South African species of <i>Lemboides</i> Stebbing and <i>Lembos</i> Bate (Amphipoda, Aoridae) described by K. H. Barnard (1916). (Published January 1987.)	267
OLSON, S. L.	
Early Pliocene ibises (Aves, Plataleidae) from south-western Cape Province, South Africa. (Published December 1985.)	57
PETHER, J. <i>see</i> KENSLEY, B.	
PICKFORD, M.	
Miocene Suidae from Arrisdrift, South West Africa-Namibia. (Published October 1987.)	283
VERSEVELDT, J. & WILLIAMS, G. C.	
A redescription of the soft coral <i>Alcyonium valdiviae</i> Kükenthal, 1906, with the description of a new species of <i>Litophyton</i> Forskål, from southern Africa (Octocorallia, Alcyonacea). (Published July 1988.)	315
WILLIAMS, G. C. <i>see</i> VERSEVELDT, J.	
WILSON, M. L.	
Notes on the nomenclature of the Khoisan. (Published August 1986.)	251

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ANNALS

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INSTRUCTIONS TO AUTHORS

1. MATERIAL should be original and not published elsewhere, in whole or in part.

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 - Number of illustrations (figures, enumerated maps and tables, in this order)
- (b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
- (c) *Table of contents* giving hierarchy of headings and subheadings
- (d) *Introduction*
- (e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
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3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 3 cm margins all round. First lines of paragraphs should be indented. Tables and a list of captions for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

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4. ILLUSTRATIONS should be reducible to a size not exceeding 12 × 18 cm (19 cm including caption); the reduction or enlargement required should be indicated (and preferably uniform); originals larger than 35 × 47 cm should not be submitted; photographs should be rectangular in shape and final size. A metric scale should appear with all illustrations, otherwise magnification or reduction should be given in the caption; if the latter, then the final reduction or enlargement should be taken into consideration.

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5. REFERENCES cited in text and synonymies should all be included in the list at the end of the paper, using the Harvard System (*ibid.*, *idem*, *loc. cit.*, *op. cit.* are not acceptable):

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- 'Smith (1969) describes . . .'
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For journal article give title of article, title of journal in italics (according to the *World list of scientific periodicals*, 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number in parentheses, pagination (first and last pages of article).

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- BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
- FISCHER, P. H. 1948. Données sur la résistance et de la vitalité des mollusques. *Journal de conchyliologie* **88** (3): 100–140.
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- KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2** (17): 309–320.
- KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* **17** (4): 1–51.
- THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

(continued inside back cover)

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ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

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Part 1 Deel



THE FOSSIL OCCURRENCE
IN SOUTHERN AFRICA OF THE
SOUTH AMERICAN INTERTIDAL MOLLUSC
CONCHOLEPAS CONCHOLEPAS

By
BRIAN KENSLEY

Cape Town Kaapstad

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THE SOUTH AMERICAN INTERTIDAL MOLLUSC
CONCHOLEPAS CONCHOLEPAS

By

BRIAN KENSLEY

*National Museum of Natural History,
Smithsonian Institution, Washington, D.C.*

(With 2 figures)

[MS accepted 16 April 1985]

ABSTRACT

The occurrence of the thaidid gastropod genus *Concholepas* is recorded from presumed Late Pleistocene coastal deposits in southern South West Africa–Namibia. The material is indistinguishable from *C. concholepas*, a species known from the Pliocene to Recent on the west coast of South America. The living species characteristically occurs in cold-temperate waters from the intertidal to depths of 40 m. It is suggested that the southern African fossils represent a short-lived pioneer population, established by larvae drifting from South America. Other organisms having a similar disjunct distribution are discussed.

CONTENTS

	PAGE
Introduction.....	1
Systematic discussion.....	2
Discussion.....	2
Acknowledgements.....	6
References.....	6

INTRODUCTION

A small collection of fossil mollusc shells from South West Africa–Namibia was submitted to the South African Museum for identification in 1983. The fossils came from Area U of the Consolidated Diamond Mines diamond area number 1, about 21 km north of the Orange River mouth.

The collection contained only three species, two of which, the bivalve *Choromytilus meridionalis*, and the whelk *Nucella squamosa*, have been recorded from the Pleistocene deposits on the west coast (see Barnard 1962; Tankard 1975). The third species is a *Concholepas*, which genus has never been recorded either as fossil or alive from Africa. On searching the Cenozoic invertebrate collections of the South African Museum, two further very worn specimens, also from South West Africa–Namibia, were found. This report describes and records this material and speculates on its history.

SYSTEMATIC DISCUSSION

Family **Thaididae**Genus *Concholepas* Lamarck*Concholepas concholepas* (Bruguière, 1789)

Figs 1, 2

Material

SAM-PQ2407, PN 33, 1 specimen, 107,6 × 75,9 mm (with adherent coarse sand and gravel); PN 34, 1 specimen, 98,3 × 72,3 mm (very worn, smooth); South West Africa, no further collection data.

SAM-PQ2408, 6 specimens, 114,4 × 90,0 mm (with attached barnacle remains), 113,6 × 81,1 mm (with attached barnacle remains), 102,2 × 78,7 mm, ? × 88,7 mm (anterior body whorl damaged), 96,0 × 73,3 mm, 48,7 × 35,2 mm (very worn); Diamond Area no. 1 of Consolidated Diamond Mines (Pty) Ltd., U11 megatranch assemblage, about 21 km north of Orange River mouth.

Description

Shell thick (up to 14 mm at outer lip of largest specimen). Entire shell of 1,5 whorls. Spire submerged, not extending beyond margin of aperture. Earliest visible sculpture cancellate, but with spiral lines stronger than axial lines; 16 spiral lines visible to siphonal ridge, weak and strong lines alternating. Body whorl expanded, aperture flared, oval, with strong siphonal groove present at anterior body whorl, ending in marginal notch; latter with two strong rounded marginal teeth projecting slightly beyond margin in unworn specimens. Outer lip margin faintly crenulate, becoming smooth in columellar region. Body whorl sculpture: 38–40 spiral ridges from apical region to siphonal ridge, 5–6 ridges below siphonal ridge, but rapidly becoming obsolete. Siphonal ridge widening distally, strongly and evenly rounded. Axial sculpture consisting of irregularly spaced growth lines, becoming wavy as margin is approached; none becoming lamellate.

Two specimens have barnacle skeletons and bases in the area of the spire, outer body whorl, as well as submarginally. The apertural margin appears aragonitic, the lining of the body whorl white and lamellar-calcareous. Two of the smaller specimens show red-brown iron-like staining.

DISCUSSION

The genus *Concholepas* contains eight recognized species or subspecies, both fossil and living. Information on geological age and distribution is well summarized in Stuardo (1979, tables 3, 4).

A brief comparative survey of these forms will help to characterize the present fossil material.

Concholepas drezi Vokes, 1972: Chipola Formation, Florida (late Lower Miocene); species with somewhat extended spire.



Fig. 1. *Concholepas concholepas*, SAM-PQ2407, inner and outer view of two specimens from South West Africa–Namibia (no further collection data available). Scale = 10 mm.

Concholepas antiquata Tate, 1894: Eocene of Mornington, Port Philip Bay, and Muddy Creek, Hamilton, Australia; species with strong terminal spire, very strong radial sculpture; aperture outline truncate due to posterior angulation.

Concholepas deshayesi Rambur, 1862: Middle Miocene of Touraine, France; species with spire of 3,25–3,5 whorls; siphonal groove ending in faint bulge on apertural margin; margin smooth, axial sculpture (growth lines) low and non-lamellar.

Concholepas kieneri Hupe, 1854: Mio–Pliocene of Chile; species with spire extending beyond aperture. (Möricke (1896) considered this species closely related to, if not a direct ancestor of, *C. concholepas*.)

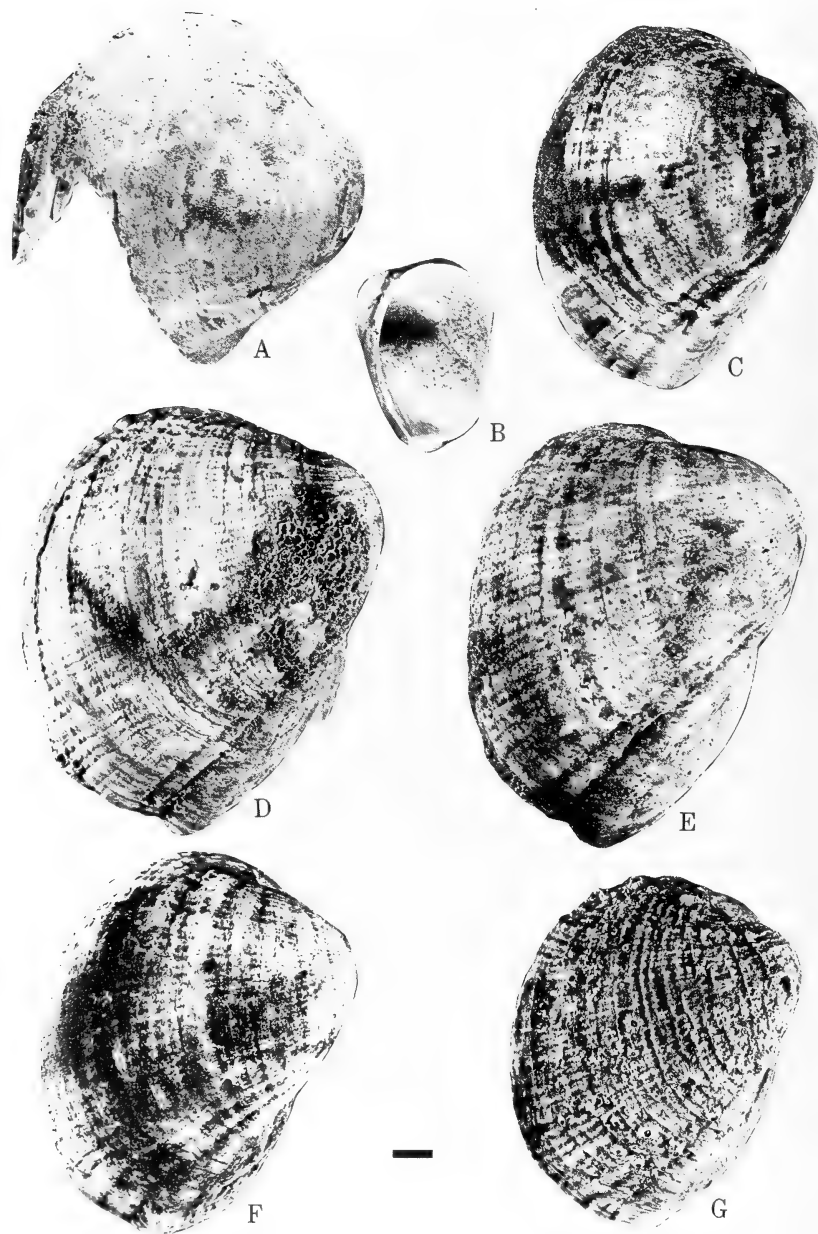


Fig. 2. *Concholepas concholepas*. A-F. SAM-PQ2408. Specimens from Diamond Area no. 1, 21 km north of Orange River mouth. G. USNM 32728, Recent specimen from Valparaiso, Chile. Scale = 10 mm.

Concholepas pehuensis (Marwick, 1926): Upper Miocene of North Taranaki, New Zealand; species subdiscoidal, with aperture wider than long. (Originally described as a *Lippistes*.)

Concholepas nodosa Möricke, 1896: Tertiary of Coquimbo, Chile; species with terminal spire, few strongly nodose spiral bands on body whorl.

Concholepas concholepas (Bruguère, 1789), and subspecies *C. c. fernandezianus* Stuardo, 1979 (confined to the Juan Fernandez Archipelago): only living representative of genus; occurring in southern Peru and along the entire coast of Chile. With the local name 'loco', the species is of economic importance as a food-source. Schwabe (1959) records the area of optimum distribution for this species as being between Valparaíso and Corral on the Chilean coast (roughly between 32° and 40°S). The species has been recorded as a fossil from the Pleistocene of Chile and Peru (Herm 1969).

Extensive studies on the morphology and variation of *C. concholepas* from South America have been done, e.g. Schwabe (1959), Lozada *et al.* (1976), and Stuardo (1979). While there would appear to be some variation in the length/width ratio of the shell aperture, most specimens fall within a cluster, as illustrated by Stuardo's figure 3. If the dimensions for the six complete southern African specimens are superimposed on Stuardo's figure 3, these too, fall within this cluster.

While axial sculpture is variable in the living *Concholepas*, with some specimens having almost lamellate ridges, in others this is less marked. Specimens from relatively circumscribed localities tend to have similar sculpture, although this is to some degree also related to ecological conditions (Herm 1969: 136).

No differences either in sculpture or proportions or morphology of the shell can be discerned between the southern African fossils and living South American specimens (of which many have been examined). There is thus no basis for taxonomically separating the southern African specimens from *C. concholepas*.

In South America, the species lives on rocky substrates from the intertidal to a depth of 40 m, usually in association with barnacles, mytilid bivalves, bryozoans, and serpulid polychaetes (Guisado & Castilla 1983). The prey is mainly barnacles and mytilids. The sea-temperature range of the species is in the region of 10–14 °C (Gallardo 1979), i.e. a temperature range similar to that occurring from the Late Pleistocene to the present on the west coast of South Africa and southern South West Africa–Namibia.

Several unanswered questions remain with regard to this record. It is unlikely that the southern African record represents a relict population of a Late Cretaceous range that included the west and south-west coasts of the separating masses of South America and Africa. There are no fossil records of *C. concholepas* earlier than the Pliocene.

What is perhaps more likely, is that the southern African fossils represent a chance pioneer population, established in the Pleistocene, long after the South Atlantic had opened up. With a pelagic life of more than two months (Gallardo 1979), larvae could be carried by the West Wind Drift from southern South

America to the west coast of southern Africa, eventually to settle on the rocky intertidal, there to prey on barnacles and bivalves. A breeding population could have been established, but which later died out either because of localized sea-level or sea-temperature fluctuations. A similar larval-dispersal argument has been used to explain the present-day southern oceanic distribution of the xanthid crab *Pilumnoides perlatus* (Kensley 1981).

A similar west coast South America–west coast southern Africa distribution has been noted for three living mytilid bivalves, viz. *Aulacomya ater*, *Choromytilus meridionalis* (? = *C. chorus* of South America), and *Semimytilus algosus*, and for the brachiopod *Disciniscus tenuis* (Kensley & Penrith 1970). Of these species, *A. ater* and *C. meridionalis* have both been recorded from the Pleistocene (Barnard 1962), the latter occurring with the *Concholepas* fossils recorded here.

ACKNOWLEDGEMENTS

I am grateful to Mr K. R. Hazell and Mr B. Hawthorne of the Geology Departments of Consolidated Diamond Mines (Pty) Ltd. and De Beers Consolidated Mines Ltd. respectively, for making the material described here available, and for collection data. Dr Louis DiSalvo of Coquimbo, Chile, provided information on literature; Dr Q. B. Hendey of the South African Museum, Cape Town, provided information and hospitality during my visits to that institution; Miss E. Pretorius took the photographs used here; to all of these, my sincere thanks. The manuscript was read by Dr R. Houbbrick (Smithsonian Institution) and Dr Q. B. Hendey (South African Museum); I am grateful for their comments and criticisms.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

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Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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e.g. '... the Figure depicting *C. namacolus* ...': '... in *C. namacolus* (Fig. 10) ...'
- The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should preferably be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

BRIAN KENSLEY

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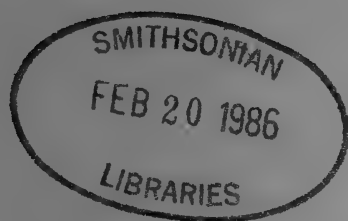
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 - (i) *Abbreviations*, where these are numerous.

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Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

Footnotes should be avoided unless they are short and essential.

Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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'Smith (1969: 36, fig. 16) describes . . .'
'As described (Smith 1969a, 1969b; Jones 1971)'
'As described (Haughton & Broom 1927) . . .'
'As described (Haughton *et al.* 1927) . . .'

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- BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
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FISCHER, P. H., DUVAL, M. & RAFFY, A. 1953. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* 74 (33): 627–634.
KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) 2 (17): 309–320.
KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* 17 (4): 1–51.
THEILE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* 4 (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* 16: 269–270.

(continued inside back cover)

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KOLPOCHOERUS PAICEAE
(MAMMALIA, SUIDAE) FROM SKURWERUG,
NEAR SALDANHA, SOUTH AFRICA, AND ITS
PALAEOENVIRONMENTAL IMPLICATIONS

By
Q. B. HENDEY
&
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Cape Town Kaapstad

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By

Q. B. HENDEY

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&

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(With 17 figures and 4 tables)

[MS accepted 1 May 1985]

ABSTRACT

A *Kolpochoerus* skull from a consolidated coastal dune at Skurwerug near Saldanha Bay is identified as an early Pleistocene representative of the southern African *K. paiceae* lineage. It is more primitive than the middle Pleistocene *K. paiceae* from the nearby Elandsfontein fossil site, and is in a comparable evolutionary state to 1,0 to 2,0 Ma *K. limnetes* from East Africa. Its suggested age is in accord with that of the high sea-level of the eustatic cycle Q2, during which the Skurwerug dune was apparently formed under circumstances similar to those that have influenced the formation of the nearby late Pleistocene-Holocene Spreeuwal dune plume. The Skurwerug *K. paiceae* suggests the presence of woodland or forest patches in the Saldanha region during the early Pleistocene.

CONTENTS

	PAGE
Introduction	9
Systematics and description	10
The Elandsfontein material	31
The Zululand specimen	39
Discussion	40
Palaeoenvironmental implications	43
Acknowledgements	53
References	53

INTRODUCTION

During 1979, the South African Museum acquired a small collection of fossil mammals from a large excavation that was being undertaken in a consolidated calcareous dune at Skurwerug, near Saldanha in the south-western Cape Province (Fig. 1). Access to the excavation was restricted for security reasons and it was not possible to determine the nature of the fossil occurrence, or to undertake a systematic investigation of the deposits from which the material was derived.

Such occurrences are not uncommon in the region and the Skurwerug specimens would have been of little interest and significance but for the fact that the collection included a particularly fine skull of an extinct pig. This specimen was found by Mr Albert W. Abraham and donated to the South African Museum by Mr P. Hutton. Other fossils from the Skurwerug excavation, which are all in a fragmentary state, were not necessarily associated with the pig skull and they will not be considered in detail here. The mammals include *Equus* cf. *capensis*, *Connochaetes* sp., *Gazella* sp. and *Raphicerus* sp.

As soon as the specimen was received it was recognized that the general morphology of the skull and cheek teeth served to place the specimen in the genus *Kolpochoerus* (formerly *Mesochœrus*) and the third molars were comparable in size with material from East Africa assigned to *K. limnetes* (Cooke 1976; Harris & White 1979). The marked reduction in the premolars indicated affinity with *K. paiceae* from South Africa but the third molars are smaller than in the large sample from Elandsfontein, suggesting that the Skurwerug specimen may be an early form of this lineage. Despite the lack of a detailed account of this specimen, it has come to be accepted as indicative of an early Pleistocene age for the coastal dune from which it was derived (Hendey 1981a, 1983a; Rogers 1982, 1983). It is the purpose of this paper to identify and describe the specimen and to consider its implications in respect of the geological succession and palaeogeography of the Saldanha region.

SYSTEMATICS AND DESCRIPTION

ORDER ARTIODACTYLA

Family Suidae

Genus *Kolpochoerus* van Hoepen & van Hoepen, 1932

Type-species: Kolpochoerus sinuosus van Hoepen & van Hoepen, 1932 (= *Kolpochoerus paiceae* (Broom, 1931)—see Cooke (1978)).

Discussion

Material assigned to *Kolpochoerus* has been recovered from many late Pliocene to middle Pleistocene localities in Africa, and it has been reviewed in recent publications by Cooke (1978), Cooke & Wilkinson (1978), White & Harris (1977), Harris & White (1979), and Harris (1983). The latter authors recognized only two valid species, whereas Cooke distinguished five. Many pig genera and species recorded prior to 1977 have been synonymized with *Kolpochoerus* and with the few species recognized by those authors cited above. The earlier nomenclatural proliferation, and the subsequent difference of opinion on the number of valid species, was due at least in part to the variation in dental characters exhibited by *Kolpochoerus* populations over its three-million-year time range so that recorded material represents temporal and, apparently, also regional variants.

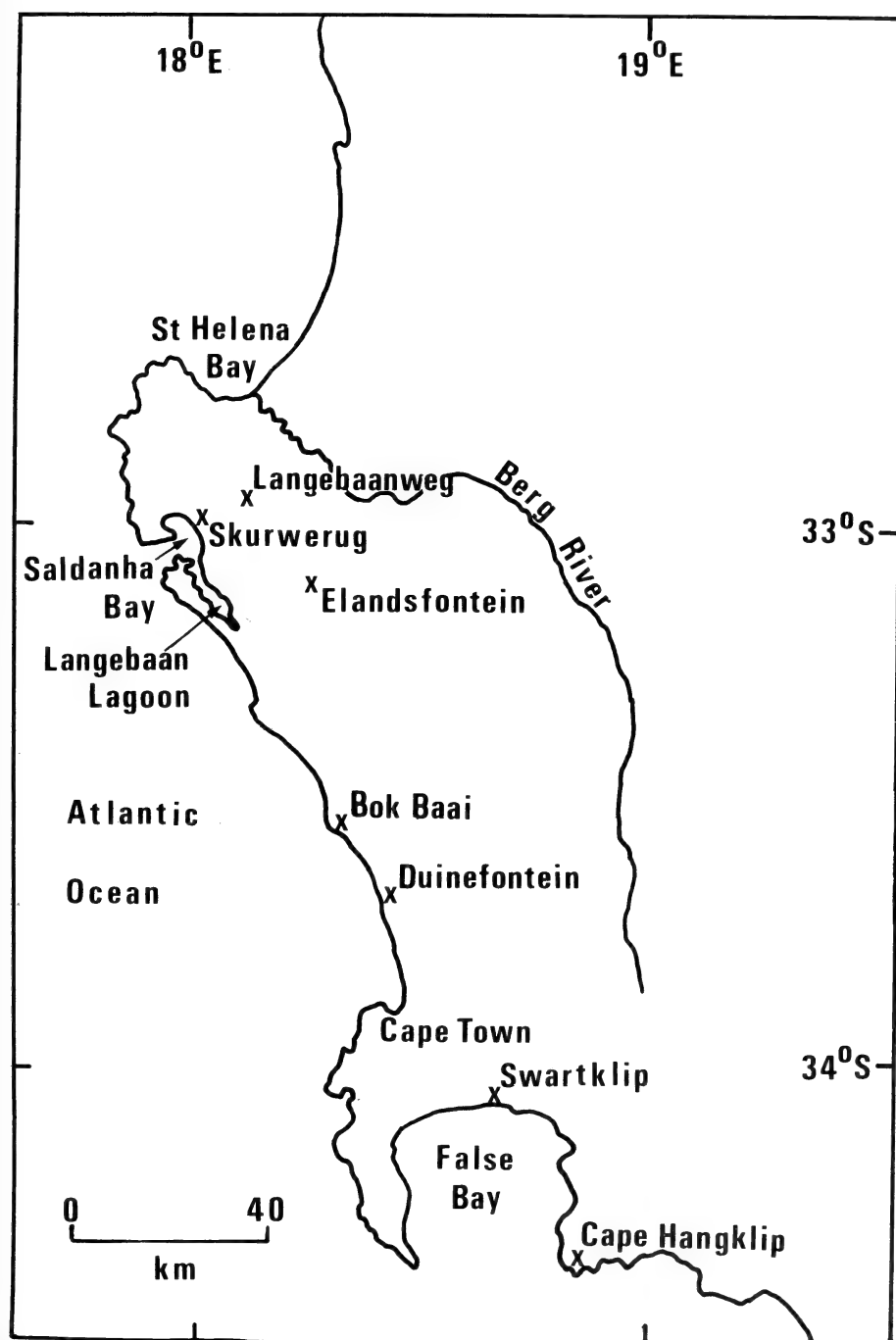


Fig. 1 The location of Skurwerug.

The only two species recognized by Harris & White (1979) are *K. limnetes* and *K. majus*. Of these, *K. limnetes* is considered to be represented by a continuum from an early form with small third molars to an 'advanced' form with elongate third molars. However, Cooke (1976, 1978) regards the advanced form as a separate species, *K. olduvaiensis*, but it would be inappropriate to debate this matter here as it is the taxonomy and not the morphology that is in question. Accordingly, to avoid unnecessary confusion in the present account, 'typical' *K. limnetes* refers to the material ascribed to this species both by Cooke and by Harris & White, while 'advanced' *Kolpochoerus* (without a species designation) denotes the advanced *K. limnetes* of Harris & White or the *K. olduvaiensis* of Cooke. *Kolpochoerus* 'majus' is contemporary with the 'advanced' *Kolpochoerus* but the third molars are in the size range of the 'typical' *K. limnetes*; they differ in being relatively more hypsodont, have more crenulated enamel and the crowns of the teeth have a distinctive lateral bulge just above the enamel line. Cooke & Wilkinson (1978) consider that the name 'majus' is a *nomen vanum* but they recognize the reality of this entity.

One of the differences of opinion referred to above concerns the recognition by Cooke (1976, 1978) of a South African lineage that is represented by the species *K. paiceae*. This species is recorded from middle Pleistocene occurrences at Elandsfontein, Cornelia, the Vaal River gravels (Cooke & Wilkinson 1978), and in Zululand (McCarthy & Orr 1978). It has hitherto been known from only fragmentary specimens, with the largest assemblage coming from Elandsfontein, which is 20 km south-east of Skurwerug (Fig. 1). This material does not show the distinctive characteristics of *K. 'majus'* but there has hitherto been only slender evidence for distinguishing it from the 'advanced' *Kolpochoerus* of East Africa. Harris & White (1979) believe that until there is an unequivocal separation of *K. paiceae* and *K. limnetes* on dental and cranial evidence, *K. limnetes* should stand as the senior synonym of a single species.

It cannot be expected that the discovery of the remains of a single individual, no matter how complete and well preserved, would settle the status of *K. paiceae*, but the Skurwerug specimen does lend support to Cooke's belief in a South African *Kolpochoerus* lineage. This specimen is evidently a more primitive form than that recorded from Elandsfontein, but it is very similar in some respects to specimens in the Elandsfontein assemblage, and to the type material from the Vaal River gravels; it is accordingly identified with *K. paiceae*.

In the final analysis, the specific identity of the Skurwerug *Kolpochoerus* is not critical since its significance lies chiefly in indicating a somewhat earlier presence of this taxon at the southern extremity of Africa than has been known hitherto, with corresponding implications in respect of the relative dating of the deposits from which it was derived.

Kolpochoerus paiceae has been known hitherto only by its dentition and by parts of the mandible so the skull characters of SAM-PQ2166 must be considered in relation to the skulls from East Africa. The general morphology of the East African material has been discussed in several papers (e.g. Cooke & Wilkinson

1978; Harris & White 1979), with the latter publication including illustrations of several specimens. These are KNM-ER 409 (pl. 10, centre, pl. 12, top), KNM-ER 212 (pl. 12, left), KNM-ER 772 (pl. 10, top), KNM-ER 788 (pls 8, 9) and KNM-ER 1085 (pl. 10, bottom), all from the Koobi Fora succession. The first two are reasonably representative of the male skull, though they are larger than the few cranial specimens from the Shungura Formation, still undescribed (Cooke & Coppens in press). KNM-ER 778 and 772 came from the upper part of the Koobi Fora succession ('*Metridiochoerus compactus*' zone) and represent the large 'advanced' *Kolpochoerus* that Cooke & Wilkinson (1978) regard as a distinct species, *Kolpochoerus olduvaiensis*. Female cranial remains are rather rare and the only female of *K. limnetes* so far illustrated is the incomplete specimen KNM-ER 1085, apart from a rather crushed skull of this species from Bed I, Olduvai (KNM-OLD FLK NNI 1235), formerly the type of *Ectopotamochoerus dubius* (Leakey, 1965, pl. 25). An almost intact undescribed large cranium from Peninj, Lake Natron, has been regarded by Cooke & Wilkinson (1978) as the female of *Kolpochoerus olduvaiensis*. Sexual dimorphism is strong, with the female having lesser development of the zygomatic arches and smaller canine flanges than in the male. The degree of difference is comparable with, or greater than, that seen in the forest hog *Hylochoerus meinertzhageni*, which is apparently the closest living relative of *Kolpochoerus* although it has special features of its own (Cooke 1976; White & Harris 1977).

Kolpochoerus paiceae (Broom, 1931)

Notochoerus paiceae Broom, 1931: 167, fig. 1

Kolpochoerus sinuosus van Hoepen & van Hoepen, 1932: 59, figs 72, 75-77. Cooke, 1974: 73, fig. 5.

Notochoerus capensis Shaw, 1939: 85, fig. 8 (*partim*).

Mesochoerus paiceae Shaw & Cooke, 1941: 293, pl. 54 (1-2). Cooke, 1949a: 35, figs 18, 19; 1949b: 44, pls 22, 23; 1976: 253, fig. 1. Keen & Singer, 1956: 352, pl. 33E. Leakey, 1958: 13. Cooke & Maglio, 1972: 310.

Metridiochoerus andrewsi Arambourg, 1943: 473 (*partim*); 1947: 352, fig. 42 (*partim*).

Tapinochoerus meadowsi Cooke, 1949a: 31, fig. 15 (*partim*).

Mesochoerus lategani Singer & Keen, 1955: 170, fig. 1. Keen & Singer, 1956: 350, pl. 33A-D. Cooke & Maglio, 1972: 310.

Kolpochoerus paiceae Cooke, 1978: 460. Cooke & Wilkinson, 1978: 462.

Mesochoerus limnetes Harris & White, 1979: 37 (*partim*).

Diagnosis

A species of *Kolpochoerus* comparable in size with the living forest hog and similar in skull size and general morphology to the 'typical' *K. limnetes* of East Africa, from which it differs in the following: relative reduction in the length of the snout and symphysis; relative elevation of the occipital condyles above the palatal plane, accompanied by reduction in height of the occiput; slight elevation of the orbits; mandibular corpus very robust; anterior border of symphysis very gently curved, resembling that of *Hylochoerus*; three pairs of lower incisors but upper reduced to two pairs; three reduced upper premolars and only two lower premolars. Third molars comparable in size and structure to those of 'advanced'

K. limnetes (*sensu* Harris & White 1979) or *K. olduvaiensis* (*sensu* Cooke & Wilkinson 1978). Male upper canines shorter and more strongly curved than in normal *K. limnetes*; female canines small but with normal open roots.

Holotype

Mandible fragment with right third molar and stump of second molar, from Vaal River gravels, Windsorton, Cape Province. McGregor Museum, Kimberley, MMK 4088.

New material

SAM-PQ2166: the incomplete skull and mandible of an adult, lacking the anterior parts of the nasals, some of the premaxillae and maxillae, all of the right and parts of the left zygomatic arches, left P¹, right P², left ascending ramus and left I₃.

Locality and horizon

Skurwerug, a consolidated dune on the farm Osfontein, 2 km inland from the eastern shore of Saldanha Bay in the south-western Cape Province. This dune is included in the Langebaan Limestone Member of the Bredasdorp Formation, as it is defined by Rogers (1983).

Description

The Skurwerug skull is that of an adult, probably female, in which all the permanent teeth are erupted, with only the most posterior pillars of the M³ talon being unworn. In size it is comparable with that of the forest hog and smaller than the male specimens from the Shungura Formation, which, in turn, are smaller than those from Koobi Fora.* Principal measurements are given in Table 1* in comparison with the earliest of the Omo male crania, L193-109 from Shungura Member C8, the smallest (KNM-ER 212) and the largest and most advanced (KNM-ER 788) of the male crania from the Koobi Fora Formation. Also included are applicable measurements for the partial female cranium KNM-ER 1085 from Koobi Fora and for the large undescribed female cranium from West Natron (Peninj),* numbered A67-384 in the collections of the National Museum of Tanzania, Dar-es-Salaam. It should be noted that these specimens cover a substantial time range.

Cranial morphology (Table 1; Figs 2, 3)

In profile the Skurwerug cranium shows the marked angulation between the rostral region and the frontals that is characteristic of *Kolpochoerus*. The back of the braincase is not unduly elevated but the occipital condyles are much higher above the palatal plane than is the case with 'typical' *K. limnetes* and this

*Personal observations by HBSC, as also are all measurements cited for East Africa; there may be minor differences from measurements given by Harris & White (1979) or by Harris (1983) but they are insignificant.

elevation is accompanied by reduction in the height of the occiput itself. This is a unique feature not seen in other specimens. The braincase itself is very slightly concave between the orbits with the orbital rim rising just above the level of the frontals, whereas in the 'typical' form they are normally below it. The cranial vault is very gently convex and broad above the temporal fossae and the temporal ridges are not strongly marked. However, the doming is less than in the 'typical' *K. limnetes* but the vault is not depressed as it is in the males of the advanced form. The morphology is very similar to the condition seen in the Peninj cranium, which suggests that there may be a sexual difference comparable to that in the living forest hog. The supra-orbital foramina are in line with, or even slightly in front of, the anterior margins of the orbits, as in the 'typical' form, whereas in the advanced form these foramina are situated a little farther back.

Although the right zygomatic arch is lost and the left one is damaged, it is clear that there was no great lateral expansion as in the males of *K. limnetes*, in which the anterior margin sweeps outwards sharply until it is more or less perpendicular to the sagittal axis. In PQ2166 the form of the zygoma is like that of the Koobi Fora female ER 1085 and not as abruptly protuberant as in the Peninj female; indeed it is rather reminiscent of the zygoma of *Sus*, although more expanded laterally. The ventral margin must have been well above the occlusal plane, so there was little of the lateral 'droop' that is seen in the early males of *K. limnetes*.

The snout is damaged and the tips of the nasals are missing but the nasal on the right side is preserved to the level of the canines. It is strongly arched in transverse section along its preserved length. The nasals were widest above the back of the canine flange and there is a distinct, but not strong, lateral projection of the nasal-maxillary junction over the infra-orbital region. In males of early *K. limnetes* the lateral projection is marked and is often accompanied by the development of rugose areas on the nasal and adjoining maxillary similar to those found in males of *Potamochoerus porcus*. These rugose areas have not been noted in the later *K. limnetes*, although the overhang persists until it disappears effectively in the advanced form. There is no sign of any rugosity in the Skurwerug specimen, as is to be expected in a female.

The right canine flange is lacking and the left one is damaged but sufficient remains to show that it was weakly developed in comparison with the strong *Potamochoerus*-like bosses seen in 'typical' male *K. limnetes*. The flange in PQ2166 curves gently out from the maxilla well in front of the infra-orbital foramen and is intermediate in form between those of female *Potamochoerus* and female *Hylochoerus*. There is a weak lateral crest about 20 mm in length that arises some 25 mm from the root of the flange at the maxilla but the flange is not at all inflated. No trace exists of any dorsal crest and it was probably absent. The canine is moderately small and emerges more or less parallel to the palatal surface. In the female cranium ER 1085 the canine flange is also small but has a marked lateral crest and there is a more prominent gutter between the front of the flange and the wall of the maxilla. In the Koobi Fora female the canine itself was



Fig. 2. Dorsal, lateral and ventral views of the *Kolpochoerus paiceae* skull from Skurwerug (SAM-PQ2166).

TABLE 1

Dimensions (in mm) of the Skurwerug cranium, SAM-PQ2166, and some other *Kolpochoerus* crania.

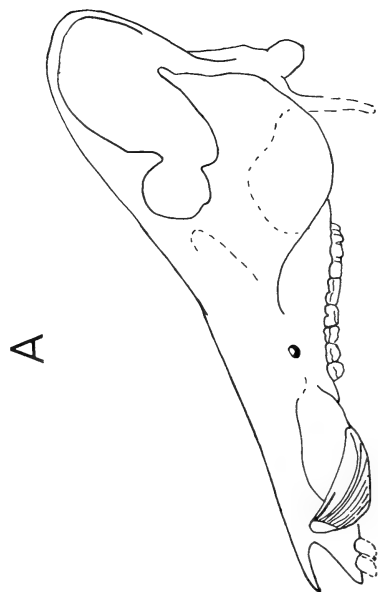
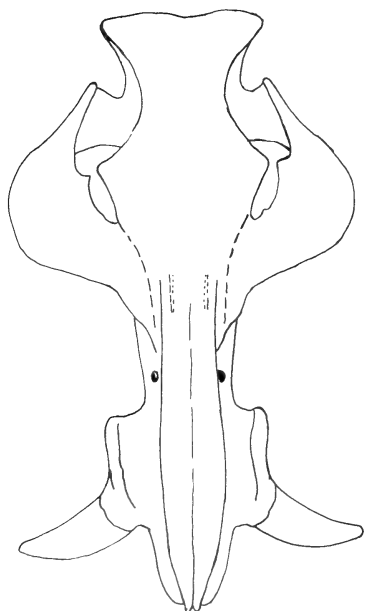
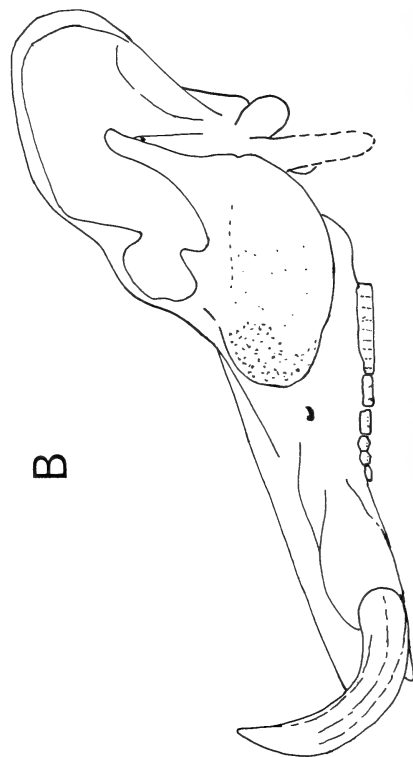
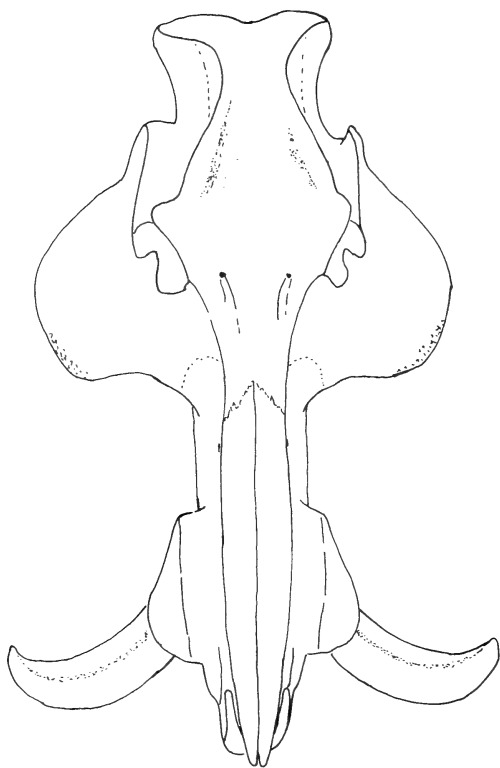
Locality	Skurwerug	Peninj	Koobi Fora			Omo
Sex	♀	♀	♀	♂	♂	♂
Number	PQ2166	A67-384	ER 1085	ER 212	ER 788	L193-109
Estimated age (Ma)	?	c. 0,9-1,3	?*	?*	1,5	2,5
Vertex length	425	553	—	505e	602	465e
Basilar length	375e	465	—	436e	483	c. 400e
Palatal length	263e	341	c. 270e	325e	354	c. 280e
Bizygomatic breadth	260	318e	—	278	364	c. 290e
Crest breadth	112	c. 150e	—	132e	145	120e
Parietal constriction	46	62e	—	65,5e	48,5	56e
Frontal breadth	134	143e	—	133	159	123e
Ocular breadth	104	125	90	108,5	110	105
Maxillary breadth at M ³	87,5	104,5	82	83	101,5	96
Post-canine breadth	c. 57	74	58e	79	84	76,5
Flange breadth	113e	123e	108e	140	180	150e
Precanine breadth	c. 78	71	—	73e	91,5	—
Height of occiput	131	212e	—	183,5	203	175e

c. = approximate; e = estimated

*The horizons for ER 1085 and ER 212 are not certain but the age is probably about 2,0 Ma ($\pm 0,5$ Ma).

also directed less laterally and slightly downwards relative to the palatal plane. In the Peninj cranium the flanges are damaged but were essentially similar except that they are distinctly tapered towards the canine root area. At the canine alveolar margin in ER 1085 the opening is about 17 mm wide and 15 mm high compared with 23 mm and 19 mm in the Skurwerug cranium; in the Peninj cranium approximate estimates are 28 mm and 23 mm respectively. In all three cases the canine had a strong dorsal groove.

The palate in 'typical' *K. limnetes* resembles that of the forest hog in general but is proportionally a little narrower. The tooth rows are usually slightly curved so that the palate is widest between the second molars and narrowest at the third molars; the anterior premolars may curve gently outwards beneath the expanded canine flanges. In PQ2166 the palate broadens anteriorly from M², much as in *Hylochoerus*. The palatine foramina, which normally lie level with the anterior pillars of M³, are slightly farther back in the Skurwerug cranium. There are two specimens of the Elandsfontein *K. paiceae* in which the palatine foramen is preserved. In one (SAM-PQ-ES5) it is positioned as in PQ2166, but in the other (SAM-PQ-ES20) it is even more posteriorly situated, being opposite the posterior pillars of the M³ trigon (Singer & Keen 1955, pls 23A, 24A). In the female cranium from Koobi Fora, KNM-ER 1085, and also in the Peninj female cranium, the palatine foramina are level with the front of M³, so this is not merely a sexual difference. In the palate of PQ2166, the U-shaped palatonarial border is situated only a short distance behind M³, which is apparently a primitive



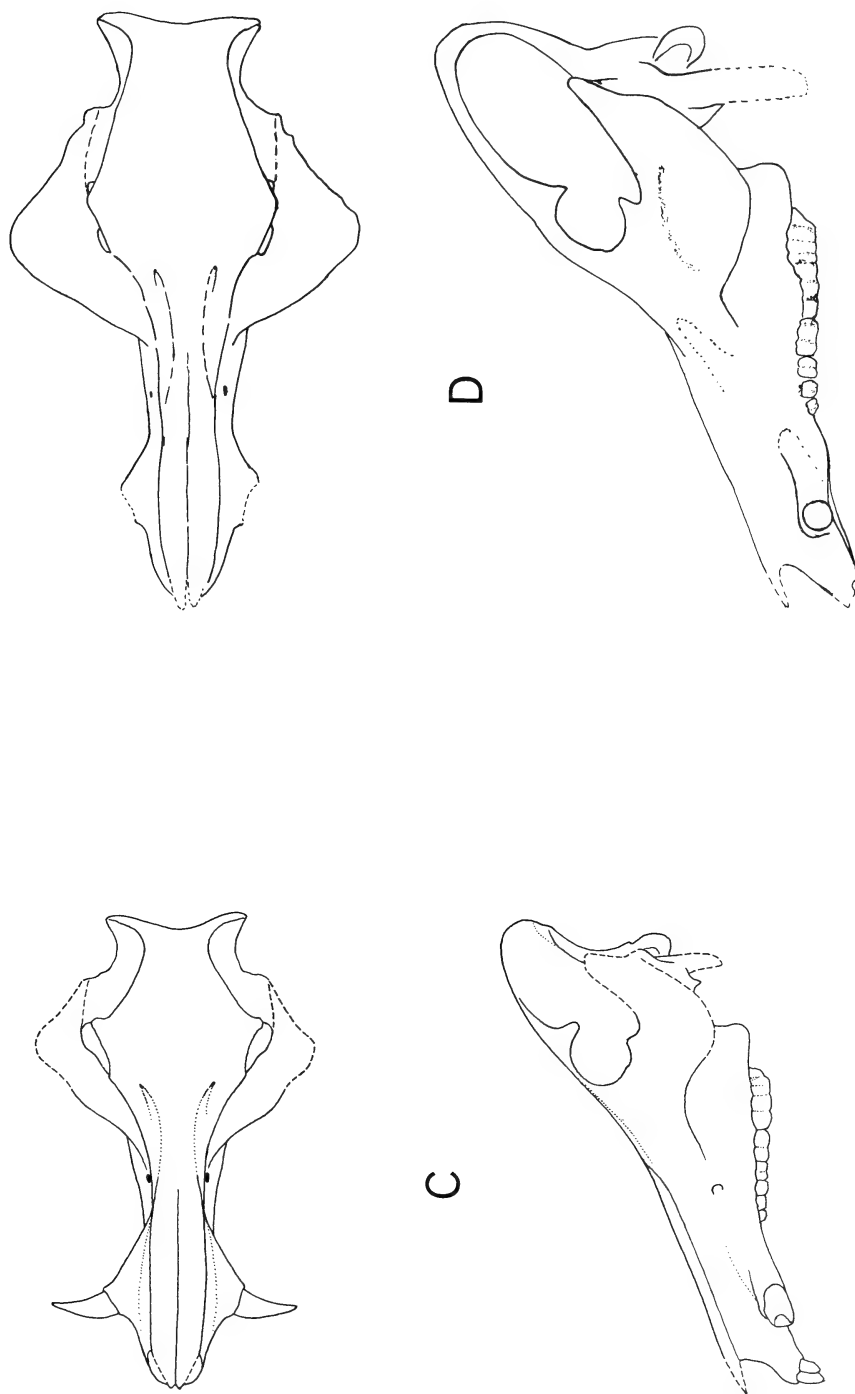


Fig. 3. *Kolpochoerus* skulls. A. 'Typical' *Kolpochoerus limnetes* (KNM-ER 409). B. 'Advanced' *Kolpochoerus limnetes* (= *olduvaiensis*) (KNM-ER 788). C. *Kolpochoerus paiceae* (SAM-PQ2166). D. 'Advanced' *Kolpochoerus limnetes* (= *olduvaiensis*) female (Penini).

characteristic, since according to Harris & White (1979) this distance is increased in advanced specimens. In the Koobi Fora female the palatonarial border is very much in the same position as in the Skurwerug cranium whereas in the Peninj cranium it extends much farther back.

The premaxilla is usually badly damaged but it is partially preserved in a few specimens of 'typical' *K. limnetes*, in the advanced Koobi Fora KNM-ER 788, KNM-ER 772 and in the Peninj cranium. It is subtriangular in shape with a rounded apex and the three incisors on each side lie almost in a straight line one behind the other as in *Sus* or *Potamochoerus*. I³ is small but is normally retained into old age, although in KNM-ER 772 it was shed during life. In PQ2166 the premaxilla is shorter and broader with a more arcuate border, only two premolars are present on each side and I² is more laterally situated in relation to I¹. There is no trace of I³ or of any scar. The I¹ and I² are essentially similar in morphology to the corresponding teeth of *Potamochoerus porcus* and to teeth attributed to *K. limnetes*.

Upper canines

The upper canines of 'typical' male *K. limnetes* somewhat resemble those of *Hylochoerus* but are shorter and relatively stouter, curving laterally at the tips with less of a backward or upward sweep than in the forest hog. There is a broad wear facet cutting across the front of the tooth. In structure the canines are also like those of *Hylochoerus*, with a strong dorsal longitudinal groove and shallower grooves on the anterior and posterior surfaces. There is a robust ventral band of ribbed enamel, a narrow inset band of smooth enamel on the anterior edge of the tusk and another on the posterior face, about 1 cm above the rear ridge of the ventral band. In *Hylochoerus* the diameter of the tusk is greater in the vertical direction whereas in *Kolpochoerus limnetes* the dimensions are about equal or the tusk is dorso-ventrally flattened. In the few specimens attributed to females, the canines are smaller, emerge with a downward and lateral component and taper at the base to form closed or nearly closed roots. The teeth are less curved than in males and the tip is cut by a small wear facet. In unworn teeth the tip of the female canine is covered with thick enamel but it thins posteriorly, extending farthest on the ventral side whereas on the dorsal side a V-shaped area of dentine extends towards the tip, coinciding with a dorsal groove in the root area. There is a good sample of both male and female canines from Olduvai Bed I in which the female canines measure about 9–10 cm in length from tip to root and the maximum and minimum diameters of the cross-section are 19–22 mm by 12–16 mm; the male canines are 20–25 cm in length, have open root areas, and cross-section diameters in the range 29–45 mm with the vertical measurement sometimes greater than the antero-posterior diameter. Male canines from the Shungura Formation up to Member G are about the same size, as also are those of 'typical' *K. limnetes* from Koobi Fora. In advanced *Kolpochoerus* the canines are longer (c. 30–35 cm) and stouter (50 mm by 39 mm in ER 788).

The canines of the Skurwerug cranium project 5 cm from the alveolar margin and the root area may occupy about another 4–5 cm. The curvature is fairly sharp and they are directed forwards and laterally almost in the palatal plane. At the alveolar margin the antero-posterior diameter is close to 24 mm and the dorso-ventral diameter 19–20 mm. There is a strong dorsal groove and weaker anterior and posterior grooves, as well as a strong ventral band of very weakly grooved enamel. There is nothing to suggest that the roots are closed. The tips are cut by a moderately broad wear facet. The size and form of these canines is thus a little more 'masculine' than are the Olduvai teeth, yet both in size and in structure they fall short of being typically male. This may be taken as indicating a degree of sexual dimorphism less marked than in 'typical' *K. limnetes* or even in the 'advanced' *Kolpochoerus* represented by the Peninj female. On the other hand, the convergence in structure is not quite as great as in female *Hylochoerus*.

TABLE 2

Dental dimensions of *Kolpochoerus paiceae* specimen, SAM-PQ2166 from Skurwerug.

	Upper		Lower	
	Left	Right	Left	Right
Length premolar series	31,2	33e	26,5	26,5
Length molar series	91,5	94,2	99,9	99e
Length cheek teeth series	123	126e	124,3	124,5e
Canine—antero-posterior diameter	24,5	23,5	21,6	22,4
—dorso-ventral diameter	18,9	20,1	18,1	18,3
—length from alveolus	51	52	67e	67
Diastema C—P ² /P ₃	47	—	57e	55,8
P2—Length (L)	8,2	lost	absent	absent
—Breadth (B)	5,0	—	—	—
—Height (H)	3,7 ⁺	—	—	—
P3—L	11,5	12,5	11,2	11,0
—B	11,0	10,3	7,0	6,9
—H	6,3 ⁺	7,4 ⁺	7,0 ⁺	8,0 ⁺
P4—L	10,7	10,3	15,2	14,6
—B	13,3	13,0	11,1	11,0
—H	5,9 ⁺	7,5 ⁺	9,0 ⁺	8,5 ⁺
M1—L	17,0s	17,4	15,9	c. 16,0s
—B	16,3s	15,2	c. 13,8	c. 14,0s
—H	d	2,5d	3,0d	3,5d
M2—L	23,0	22,2	23,7	23,2
—B	20,7	19,9	17,8	17,8
—H	20,0 ⁺	12,5 ⁺	8,5 ⁺	8,0 ⁺
M3—L	50,0	53,1	60,2	60,0e
—B	25,0	24,1	29,2	29,7
—H	25,0	25,0	21,0	22,0
—Trigon(id) length	28,7	29,8	29,2	29,7

c. = approximate; e = estimated; s = stump; d = mainly dentine

⁺ = incomplete (worn)

Upper cheek teeth (Table 2; Figs 2, 4, 5)

The upper dentition of the Skurwerug cranium is remarkable not only in having the incisors reduced in number (to two pairs) but also in having the premolars reduced both in size and in number (to three upper and two lower pairs). The Peninj cranium has the upper premolars reduced to only two pairs, but they are relatively enlarged rather than reduced. PQ2166 shows no sign of P¹, nor of any scar to indicate that it was ever present. In *K. limnetes* P¹ was present in the rare female specimen KNM-ER 1085 (although only the socket remains) and in the Olduvai Bed I palate FLK W 626, so its retention may well have been a normal feature in the 'typical' female. Although it is lacking in many of the male specimens, it is certainly present in some cases. At Olduvai it occurs in a crushed male skull FLK NN I 177, lying 0,5 cm in front of P², as in the female skull mentioned above; at Koobi Fora it was present in the male skull KNM-ER 212, lying in contact with P²; and in the Shungura Formation was present in the male cranium L193-109 from Member C8, lying 2,5 cm in front of P².



Fig. 4. Occlusal view of the left upper cheek teeth of the *Kolpochoerus paiceae* skull from Skurwerug (SAM-PQ2166). Natural size.

The P² of PQ2166, which is preserved on the left side only, has the exposed parts of its two roots fused. The normal P² has three cusps, one behind the other, with the central cusp the largest. In PQ2166 there are only two cusps, well fused and worn so that the dentine areas almost merge. The anterior cusp is longer than the posterior one and tapers anteriorly, giving it a triangular outline in occlusal view. It somewhat resembles the P¹ of other specimens although the true P¹ is single-rooted.

The right P³ is intact, that on the left slightly damaged, and both are well worn. The tooth is triangular in occlusal view, with one root anteriorly and two roots posteriorly. There is a large main cusp (paracone) on the labial side, another postero-lingually (hypocone), and a very small cusp posteriorly. An apparently small distinct cusp anteriorly has been linked to the central cusp

through wear. The rather *Sus*-like arrangement is normal for *Kolpochoerus limnetes* but the tooth is considerably smaller than in any of the other material referred to this species (Fig. 5).

The P⁴ has a more complex crown, with an almost molariform morphology. It apparently has three roots, and the tooth is broader posteriorly. The crown morphology is somewhat obscured by wear and is most clearly seen in the right P⁴. There are two pairs of more or less equally sized cusps anteriorly and posteriorly, and a small accessory cusp situated medially on the lingual side. There is a posterior cingulum. The enamel of the principal cusps is slightly crenulated. The teeth of 'typical' *K. limnetes* are normally dominated by the enlarged paracone and protocone with a lesser metacone; cingular cusps are commonly developed and add to the complexity of the pattern but the essentially quadritubercular pattern seen in the Skurwerug dentition has not been noted in the East African material. The P⁴ is substantially smaller than in any of the East African specimens (Fig. 5).

Both left and right M¹ of PQ2166 are heavily worn and details of their cusp morphology are no longer discernible. However, it is clear that this more or less rectangular tooth has paired roots anteriorly and posteriorly that supported paired cusps in an arrangement that is typical of the M¹ of *Kolpochoerus* and other pigs.

The M² of PQ2166 also has a typically *Kolpochoerus* morphology. This tooth has paired roots anteriorly and posteriorly, supporting paired cusps that are separated by a smaller median cusp, and flanked anteriorly and posteriorly by well-developed cingula that are fused with small median cusps. In size both M¹ and M² lie near the bottom of the range of East African *K. limnetes* material (Fig. 5).

In PQ2166, the M³ have the pillar-like structure that is characteristic of *Kolpochoerus*. The trigon is morphologically similar to M², and consists of two sets of paired cusps separated by a smaller median cusp, an anterior cingulum that is fused to a small median cusp, and another small median cusp posteriorly. The trigon cusps are crenulated. The talon is shorter than the trigon and its cusps are less symmetrically arranged. The most anterior of the talon cusps is a median one that abuts the posterior median cusp of the trigon. It is flanked by a smaller buccal cusp and a more posteriorly situated and larger lingual cusp. This arrangement is repeated in a second row of slightly smaller cusps. Finally, there is a single postero-buccal cusp on the left M³. There is no crenulation of the talon cusps. The M³ has a heavier cement cover than M². In size the teeth are appreciably smaller than all of those from Elandsfontein and fall well within the range for the sample from Olduvai Bed I (Fig. 5), or that from the Shungura Formation, Member G.

Mandible

The general form and characteristics of the mandible of PQ2166 conform to those seen in 'typical' *K. limnetes* but there are differences in the shape and proportions of the symphysis and in the reduction of the premolars in the

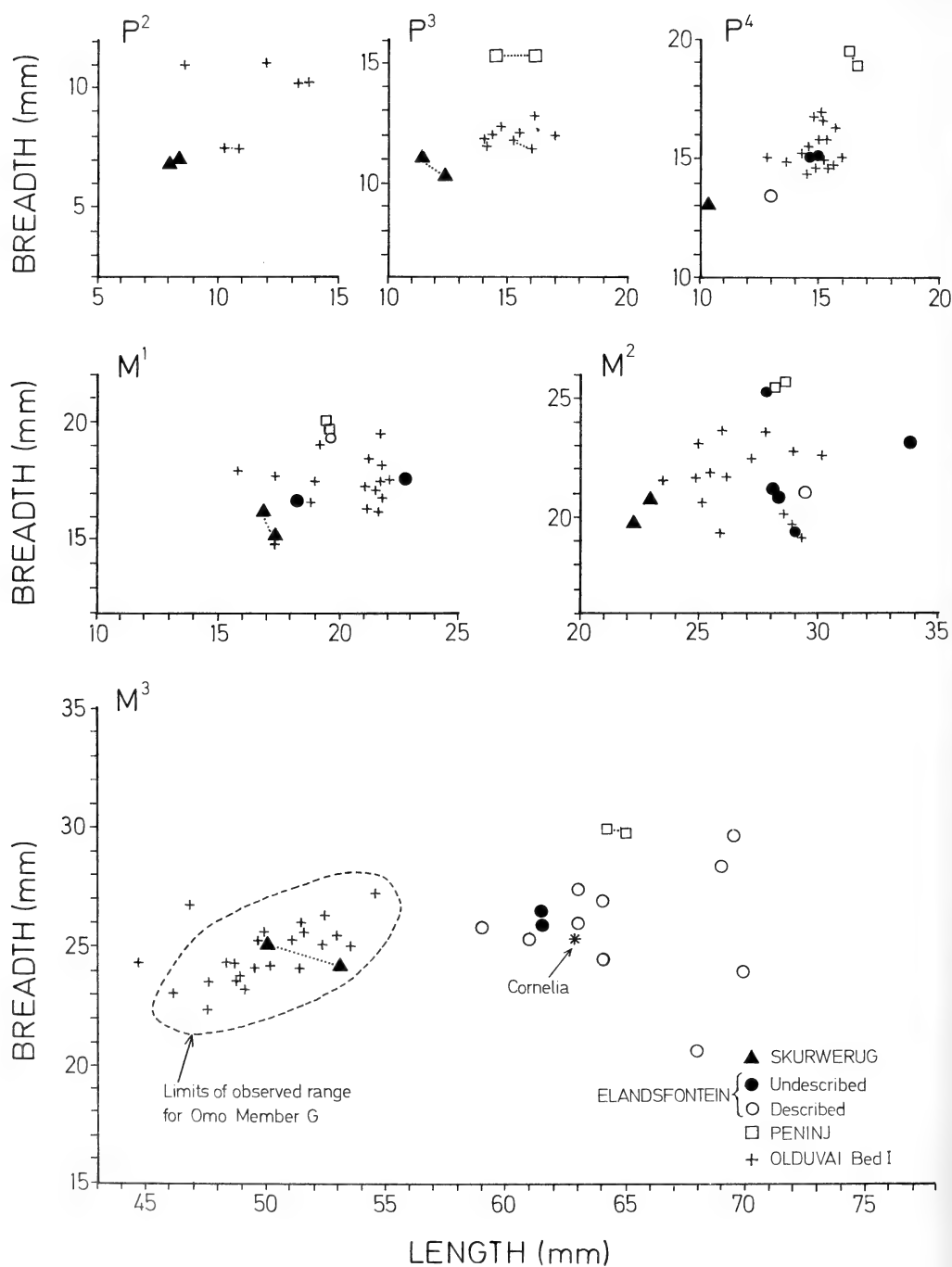


Fig. 5. Length/breadth measurements of upper cheek teeth of *Kolpochoerus paiceae* from Skurwerug, Elandsfontein and Cornelia, *K. limnetes* from Olduvai Bed I, and an advanced *Kolpochoerus* from Peninj.

TABLE 3
Dimensions of the Skurwerug mandible, SAM-PQ2166,
and some other *Kolpochoerus* mandibles.

Locality Number	Skurwerug		Elandsfontein		Olduvai		Koobi Fora		Omo	
	PQ2166	E20928	E16675	BM.M 17079 MMK III/IV	1000 FLK NN I	ER 946	ER 1314	OMO 27-3	OMO L64-5	
Estimated age (Ma)	?	c. 0,8	c. 0,8	c. 0,8	1,8	c. 1,7	?	2,0	2,5	
Total length	352	—	—	416	—	461	355	—	—	
Height of condyles	146	—	—	—	—	194	184	—	—	
Length of symphysis	101	c. 106	c. 106	139	115	146	125	145	114	
Canine flange breadth	93,5e	110e	102	136	92	129,5	104	129	112	
Constriction	73,5	95	86	92	73	101	93	97,5	85	
Jaw height at P ₄ /M ₁	64,5	68e	c. 66	76,5	57	65,5	61	c. 65	64,5	
Jaw thickness at M ₂ /M ₃	44	55	56e	43	43	55	46	c. 55	51	
Diastema C-P	56	62e	75e	91	62	96	81	69	85	
Premolar series	26,5	25e	c. 25	29+	38	42,5	41	46,5	42,5	
Molar series	99,9	c. 110	—	122,6	87,8	111	104	106	99,6	

c. = approximate; e = estimated

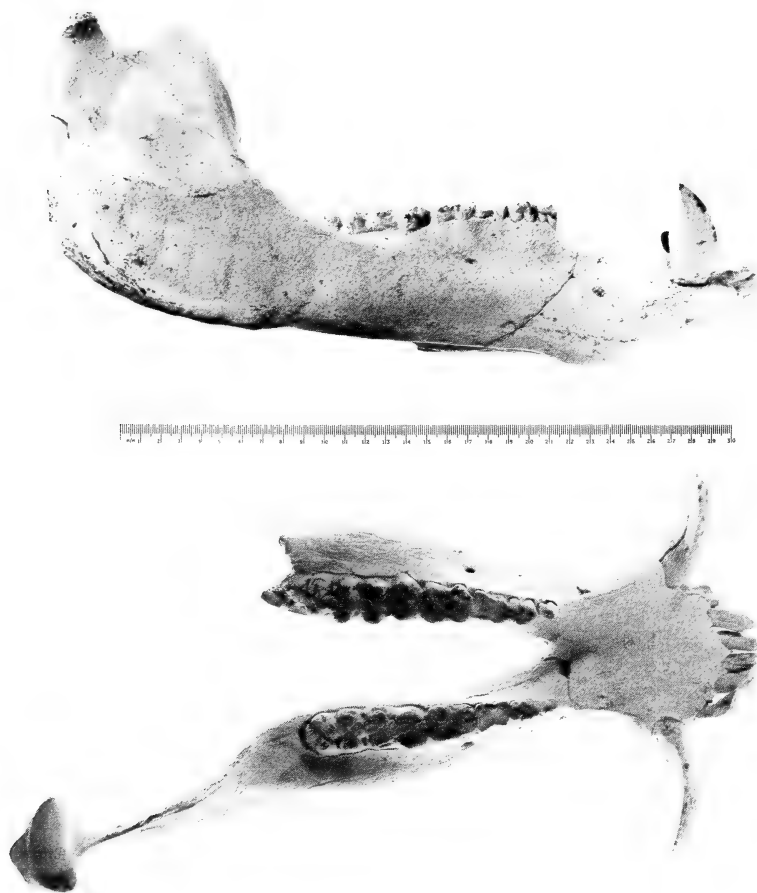


Fig. 6. Lateral and dorsal views of the *Kolpochoerus paiceae* mandible from Skurwerug (SAM-PQ2166).

Skurwerug specimen. *Kolpochoerus* shares with *Hylochoerus* a stout mandible with great width across the canines, only modest constriction behind them, and inflation of the corpus lateral to P₄, narrowing again fairly abruptly opposite the middle of M₃. In *Hylochoerus* the mandible of the female is a little less robust than in the male but the differences are slight. In the forest hog the breadth across the canines is about the same as the length of the symphysis—relatively slightly narrower in females—whereas in *Kolpochoerus limnetes* the symphysis is longer than the breadth across the canines. In the forest hog the back of the symphysis lies well in front of the anterior premolar and the gap between it and the back of the canine is about equal to the sum of the lengths of the three molars; in ‘typical’ *K. limnetes* the symphysis begins about level with the anterior premolar and the gap is about as long as the third molar, or a little longer. In the forest hog the

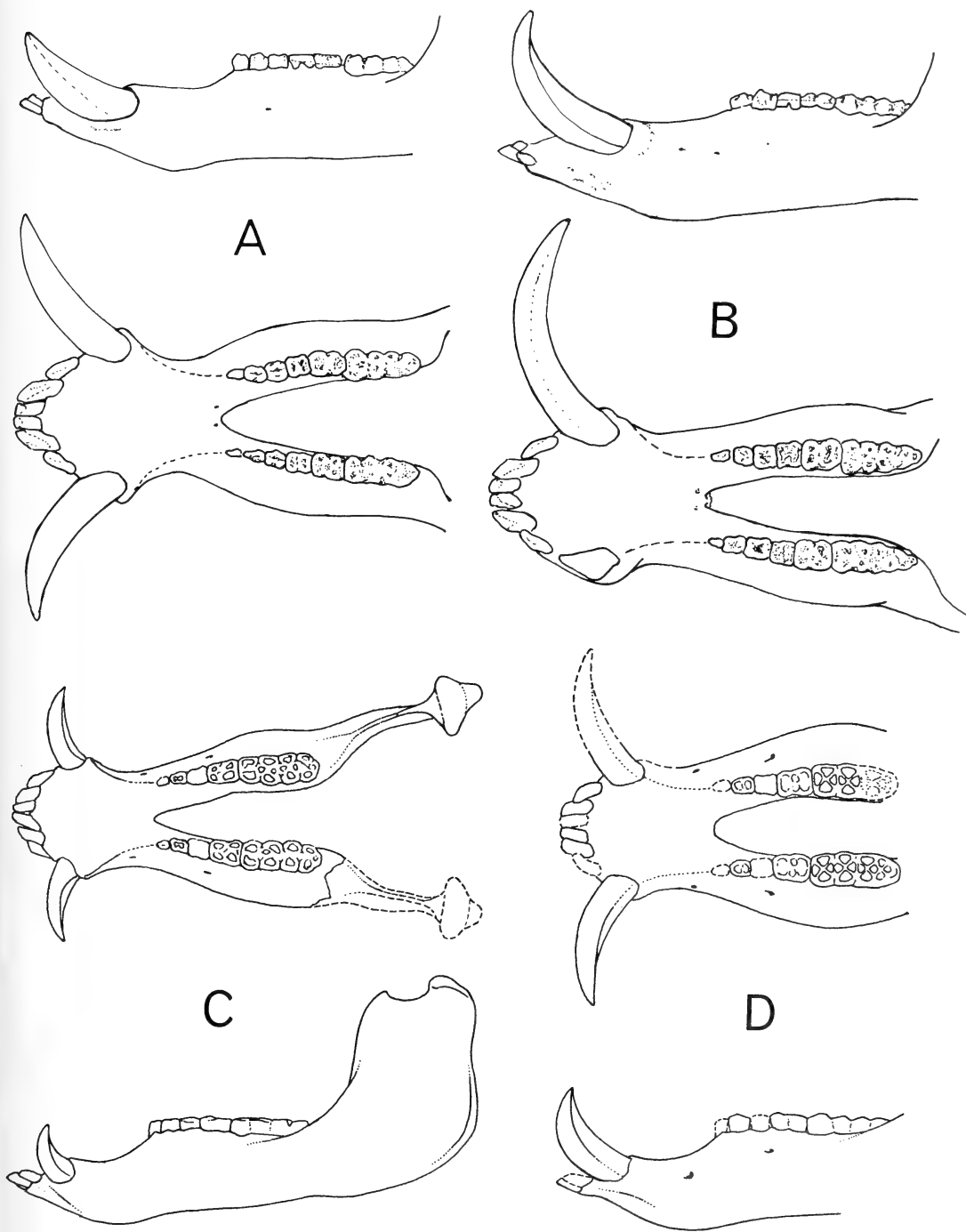


Fig. 7. *Kolpochoerus* mandibles. A. 'Typical' *Kolpochoerus limnetes* (Omo L64-5 and incisors of L36-27). B. 'Advanced' *Kolpochoerus limnetes* (= *olduvaiensis*) (KNM-ER 1314). C. *Kolpochoerus paiceae* (SAM-PQ2166). D. *Kolpochoerus paiceae* (SAM-PQ-E16675 and E20928).

anterior border of the symphysis is only slightly curved whereas in *K. limnetes* it is more nearly semicircular and thus extends farther in front of the canines. The junction of the two rami lies slightly below the lower surface of the corpus in *K. limnetes* and the symphysis rises gently to the incisor border, almost as a straight line in profile, although there is a very weak shelf supporting the procumbent incisors, much as in *Hylochoerus*.

Compared with 'typical' *Kolpochoerus limnetes*, the Skurwerug mandible has a shorter symphysis, only very slightly longer than the breadth across the canines, but its origin is still about level with the front of the premolars. The distance from the front of the premolars to the back of the canine is also reduced, being very slightly less than the length of the M_3 alone. The anterior border of the symphysis is less arcuate, although not as flattened as in *Hylochoerus*. The profile of the symphysis is rounded, very much as in *Phacochoerus* and, like the latter, the incisors are set in a shelf-like projection. All three pairs of incisors are retained, with I_3 not reduced (as it is in *Hylochoerus*) and the structure of the incisors is basically similar to that in *Sus*, but perhaps closer to that of *Hylochoerus*. The ascending ramus is a little different from the few *K. limnetes* jaws in which it is preserved, for in these specimens the anterior edge is more upright than in PQ2166 and antero-posteriorly narrower, especially in the 'advanced' form (e.g. see Harris & White 1979, pl. 11—KNM-ER 1314). In PQ2166, also, the rear edge of the ascending ramus is farther back from the end of the cheek teeth, giving a 'stretched-out' appearance to the ascending ramus. The height to the condyle is also less than in 'typical' *K. limnetes* and considerably less than in the advanced form. Some measurements covering a substantial time range are given in Table 3.

The lower dentition (Table 2; Figs 2, 8, 9)

The lower canines of PQ2166 emerge from the symphysis almost perpendicular to the axis of the mandible and rise at a low angle, which is typical of *Kolpochoerus limnetes*. They extend 6 to 7 cm from the alveolar border and are very similar to the canines from Olduvai Bed I that are attributed to females, although perhaps a little more robust. The cross-section is subtriangular with a somewhat rounded anterior keel. The posterior facet is 18 mm broad at the alveolar margin, the antero-dorsal facet 21 mm broad and the antero-ventral one 22 mm. The two larger faces are covered with thin enamel that is weakly striated longitudinally. There is a strong wear facet 4–5 cm long on the back of the tooth. There are no anterior wear facets indicative of extensive digging.

The lower premolars of PQ2166 are reduced in size and number compared with the 'typical' East African *K. limnetes*, in which P_2 is almost invariably present although in the 'advanced' form it may be shed in the mature adult. Only in one 'advanced' specimen from Koobi Fora, KNM-ER 6, is P_2 apparently absent and P_3 is slightly reduced in size, but the P_4 is normal.

The P_3 of PQ2166 is a simple double-rooted tooth that is morphologically a stouter version of the upper P^2 . The anterior root is stouter and longer than the



Fig. 8. Occlusal view of the right lower cheek teeth of the *Kolpochoerus paiceae* mandible from Skurwerug (SAM-PQ2166). Natural size.

posterior one, and the anteriorly tapering part of the crown which it supports is correspondingly longer, but narrower, than the posterior section. A single elongated dentine island has been exposed by wear. In *K. limnetes* there is a stout main central cone linked to a well-developed posterior cingulum cone and to a weak anterior cingulum cusp. In PQ2166 the anterior cingulum cusp is lacking.

The P₄ of PQ2166 is a double-rooted tooth that is appreciably larger than P₃. The P₄ is well worn in both halves of the mandible, and the occlusal surfaces are taken up by figure-of-eight exposures of dentine, flanked anteriorly by a prominent cingulum. The characteristic offset of the double central cusp is apparent and the pattern is normal for *Kolpochoerus limnetes*, though the crown tapers a little anteriorly as compared with the usual rather rectangular crown. The reduction in size of P₃ and P₄ in comparison with the sample from Olduvai Bed I is clear from Figure 9.

Both left and right M₁ of PQ2166 are well worn, the only enamel remaining being on the lingual surfaces of these teeth. They evidently had paired cusps anteriorly and posteriorly, the latter being slightly the broader.

The left and right M₂ are also heavily worn, but sufficient enamel remains on the occlusal surface to show that the cusps consist of anterior and posterior pairs, separated by the two median cusps, and flanked by anterior and posterior cingula. The M₁ and M₂ are at the low end of the size range for the Olduvai Bed I sample but are otherwise unremarkable (Fig. 9).

In the M₃ of PQ2166, the trigonid and talonid are of similar size and, except for the anterior cingulum of the trigonid, they are nearly replicas of one another. Except for its slightly larger size and absence of a posterior cingulum, the M₃ trigonid is similar to M₂, with paired cusps anteriorly and posteriorly separated by two median cusps, with two other median cusps anteriorly and posteriorly. This paired cross-shaped cluster of four cusps is also the pattern of the talonid, although there is an additional small cusp developed postero-lingually on the

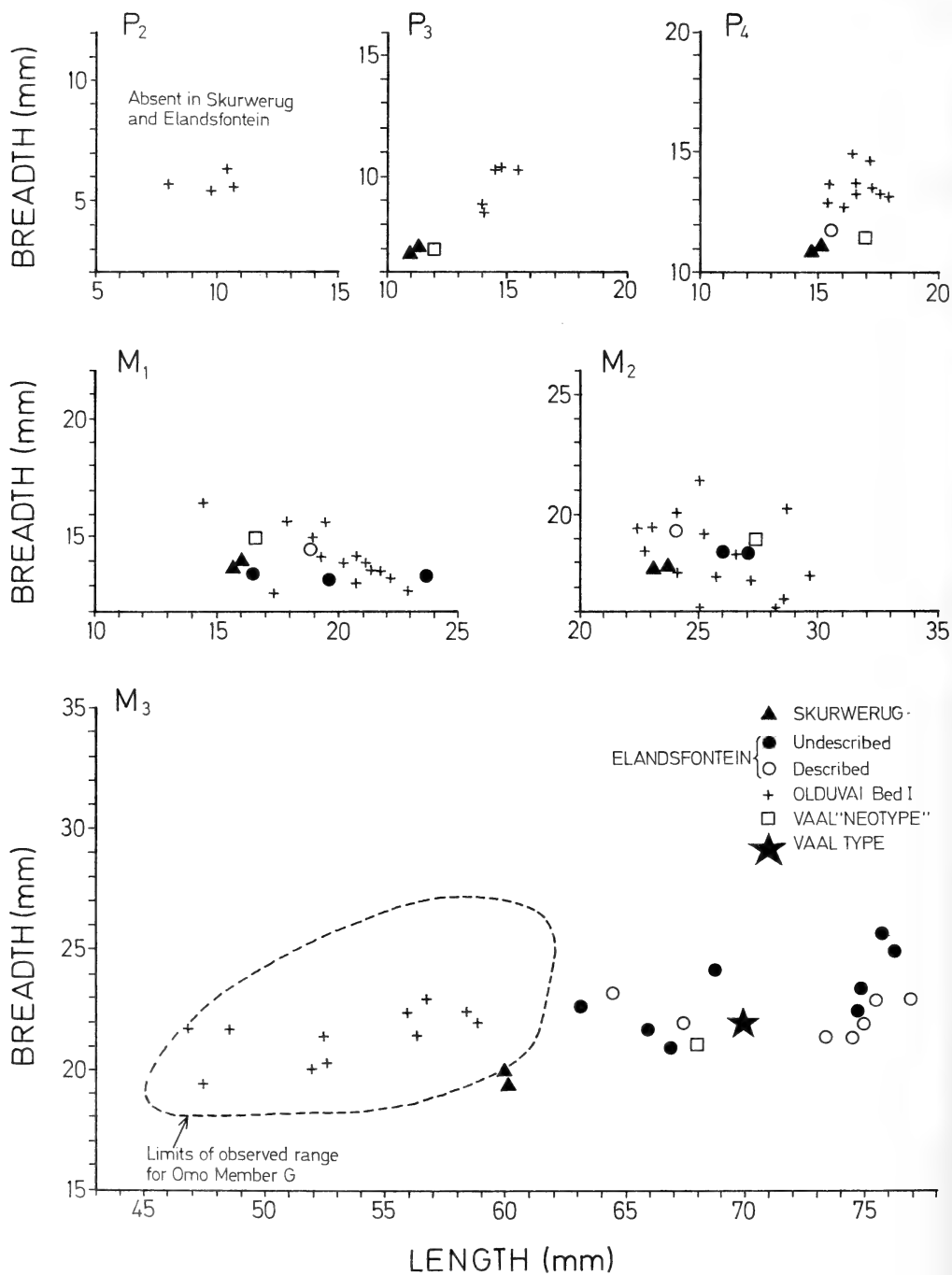


Fig. 9. Length/breadth measurements of lower cheek teeth of *Kolpochoerus paiceae* from Skurwerug, Elandsfontein and the Vaal River gravels, *K. limnetes* from Olduvai Bed I, and an advanced *Kolpochoerus* from Peninj.

most posterior median cusp. The presence of four pairs of laterals is a moderately advanced characteristic and the M_3 lies at or just above the upper limit for the Olduvai Bed I sample (Fig. 9). The crown height is not abnormal for teeth at this stage in the lineage.

THE ELANDSFONTEIN MATERIAL

Figs 7D, 10–14

Singer & Keen (1955) described a small collection of suid remains from the farm Elandsfontein, the locality from which the 'Saldanha' hominid skull had been recovered (Drennan 1953); the site is often referred to in the literature as 'Hopefield'. The material consisted of jaw fragments and teeth apparently representing the remains of 12 individuals. Comparisons were made with the then known material of *Mesochcerus olduvaiensis* and a new species was created, *M. lategani*, with the type consisting of seven fragments comprising an incomplete set of upper and lower cheek teeth of a single animal. Keen & Singer (1956) added descriptions of four more third molars referred to *M. lategani* and also a mandibular fragment with RM_3 (ES28), which they referred to *M. paiceae*; they also removed the previously described M_3 (ES21) and referred it to *M. paiceae*. A left mandibular fragment with an unworn M_1 , D_4 and part of D_3 was referred to *Mesochcerus* but not named specifically. The 1956 collection also included the upper second and third molars (ES26) of a much larger suid referred to what was then called *Tapinochoerus meadowsi* but Harris & White (1979) refer it to *Metridiochoerus compactus* (= *Stylochoerus compactus* of Cooke & Wilkinson 1978). Three additional incomplete third molars (E9171, 11765 and 12040) have since been recovered and serve to confirm this identification. The age of the bulk of the Elandsfontein fauna is assessed as approximately coeval with the upper part of the Olduvai succession (Bed III or IV), but it also includes younger elements, and some material may even be older (Hendey 1974).

Subsequent to these accounts, additional material referable to *Kolpochoerus* has been recovered, mostly pieces of maxilla or mandible with two or three cheek teeth, and a few isolated molars and canines. The most complete specimens are two partial maxillae of one individual with RP^3-M^3 and LP^4-M^3 (E16550A, B) and two rather damaged mandibles (E16675 and E20928), which include the symphyseal areas. Measurements on all the teeth are plotted in Figures 5 and 9, with the described and undescribed material distinguished by open and solid circles respectively. Although few of the premolars are preserved intact, the roots or sockets are present on several specimens and demonstrate the same reduction in numbers and size as are displayed by the Skurwerug skull.

No upper incisors are known in the Elandsfontein collection but there are three upper canines—a pair E16297 (Fig. 10) and a poorly preserved specimen E11808. These specimens are appreciably stouter than the upper canines of the Skurwerug cranium; they are considerably shorter than normal males of *K. limnetes* but they probably do belong to male animals as they are too big to be



Fig. 10. Ventral and dorsal views of left and right upper canines respectively of *Kolpochoerus paiceae* from Elandsfontein (SAM-PQ-E16297).

female. Nevertheless, they are very different from the strongly flared hylochoerine to phacochoerine ones of 'advanced' *Kolpochoerus* (e.g. KNM-ER 788 in Harris & White 1979, pl. 9) and, as the Elandsfontein deposit is almost certainly coeval with very advanced *Kolpochoerus* in Olduvai Beds III and IV, this is regarded as a significant feature of *K. paiceae*.

The P³ is known only by the posterior root in the maxilla of E16550A (Fig. 11). The entire tooth is estimated to have been about 13 mm long and 11 mm wide, or very slightly larger than in the Skurwerug cranium. The P⁴ is also present in this specimen and its mate in E16550B. They are also slightly larger than in PQ2166 but are structurally similar in having a molariform aspect. There is an

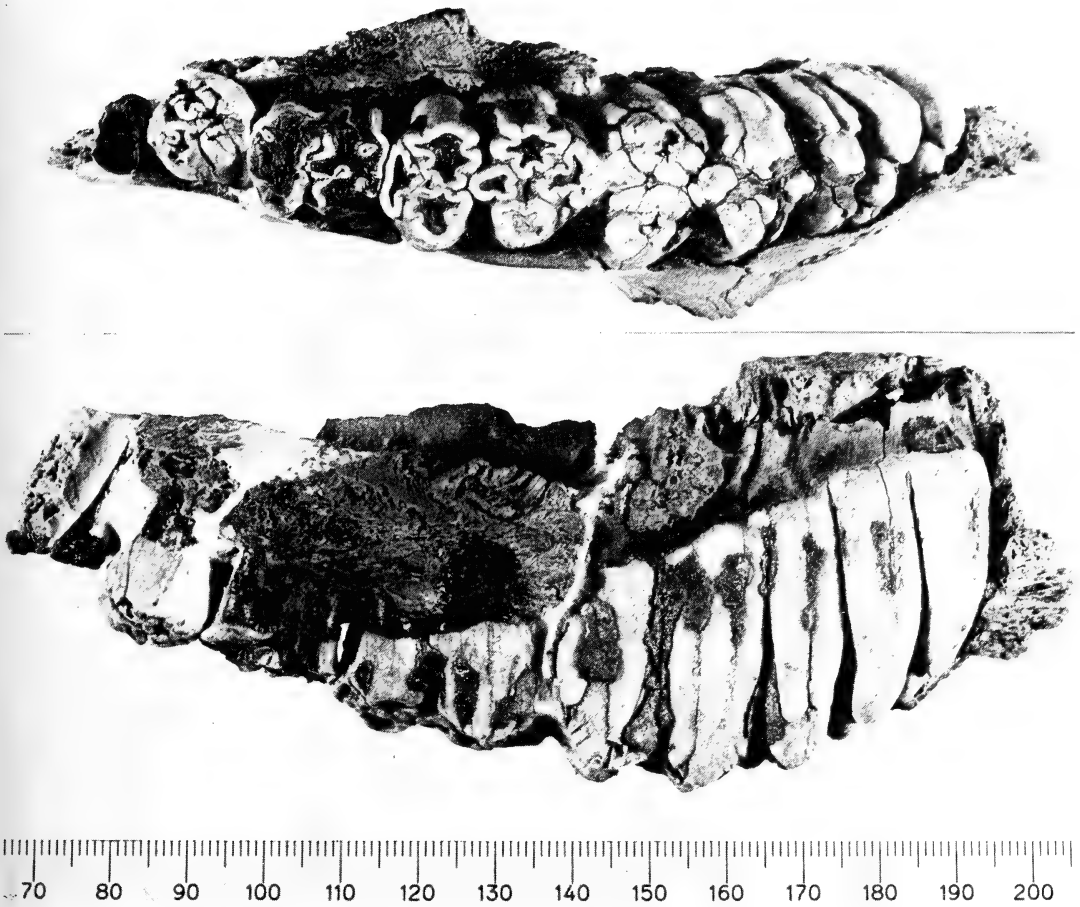


Fig. 11. Lingual and occlusal views of the right upper cheek teeth of *Kolpochoerus paiceae* from Elandsfontein (SAM-PQ-E16550).

anterior cingulum made up of four small cusps, paired cusps anteriorly and posteriorly that are separated by a small median cusp, and a reduced posterior cingulum made up of two small cusps. The process of molarization is not carried quite as far as in *Hylochoerus* but the trend is similar. The only other P⁴ is in a maxilla fragment (ES7) but in this specimen the configuration is more normal for *Kolpochoerus* with two buccal cusps, one lingual cusp, and anterior and posterior cingula that are made up of several smaller cusps (Singer & Keen 1955, pl. 23D). The enamel of the principal cusps is more crenulated than in the P⁴ of PQ2166.

The upper first molar is preserved in E16550A (Fig. 11) but is broken away in its mate. Although the fundamental pillar structure is normal, the tooth is worn to the point at which large areas of dentine are exposed, together with ribbons and rings of enamel; the M³ in this specimen is still incompletely erupted with only the

front pillars in wear, so the extent of the wear on M^1 is a little surprising. M^1 is also present in ES7 in which the wear is a little less advanced and the structure is normal (Singer & Keen 1955, pl. 23D).

There are five examples of M^2 , in various stages of wear, and they are essentially similar to the teeth of 'typical' *K. limnetes*. The enamel of the principal cusps is more crenulated than in PQ2166 and there is a heavier covering of cement, both of which Harris & White (1979) regard as progressive characteristics. Another specimen, E2647/8, has the M^1 and M^2 worn at an unusual angle, apparently due to abnormality in eruption.

There are 17 examples of M^3 , some of them incomplete but 12 are measurable and represent at least 10 individuals. Length/breadth plots are given in Figure 5. The teeth are all larger than the M^3 of the Skurwerug cranium, carry a heavier coating of cement, and are relatively higher crowned. Most of the specimens have three pairs of lateral pillars with a terminal complex that may include an incipient fourth pair of laterals. One of the smaller specimens, ES23 (Keen & Singer 1956, pl. 33A) is unusual in having a total of only four pillars on the talonid, namely a small median, the third pair of laterals, and a stout terminal pillar. The smallest tooth, ES24, has the same arrangement of pillars as in the Skurwerug cranium, although the crown is 6 mm longer. The third molars in the pair of maxillae, ES16550, are similar in size to ES23 and ES24 yet have four fully developed pairs of laterals and a pair of terminal pillars of smaller size (Fig. 11). The unworn third pair of laterals have a height of 36 mm. The largest teeth are a pair, ES14 and ES15, in which the fourth pair of lateral pillars is quite well developed, plus a small double terminal pillar (Singer & Keen 1955, pl. 21A). ES15 reaches a crown height of 42 mm on the unworn second lateral pillars. In contrast, ES27 is equally large yet has only three pairs of laterals and a terminal complex of smaller pillars (Keen & Singer 1956, pl. 33D). There is thus a good deal of variation within the Elandsfontein sample, more so than in samples from limited time zones in East Africa, perhaps because the former is temporally heterogeneous.

Although there are a number of fragments of the lower jaw, there are only two specimens that demonstrate the morphology. E16675 has the entire symphysis preserved, with some damage to the incisor area, but retaining parts of both canines (Fig. 12). The right ramus is lacking but the left ramus is preserved as far back as the contact with the front of M_3 . Unfortunately the cheek teeth were lost post mortem but the root sockets allow some inferences to be made. P_2 was clearly absent, the roots of P_3 are very small and P_3 and P_4 together occupied a total of 25 mm, while the roots of M_1 and M_2 have a combined length of about 49 mm. The symphysis is slightly longer than in the Skurwerug mandible, and the breadths across the canine flanges and across the post-canine constriction are also greater in E16675 (Table 3). The back of the symphysis lies a little in front of the P_3 . The cross-section of the canines is about the same size as in PQ2166 but they appear to have been considerably longer. It seems likely that the jaw is either that of a young male or, more probably, of a female more robust than PQ2166. The



Fig. 12. Dorsal view of *Kolpochoerus paiceae* mandible from Elandsfontein (SAM-PQ-E16675).

second mandible, E20928, was shattered and the relative positions of the two horizontal rami are slightly distorted in the reconstructed specimen, but it is clear that it was very similar to E16675 (Fig. 13). The canines are appreciably larger and it is virtually certain that this was a male animal. In the two specimens the symphysis is identical in length and a reliable estimate of the breadth across the canines in E20928 is slightly more than in E16675. The back of the symphysis is in the same relative position and both have a curved profile to the symphysis with a projecting shelf for the incisors. The gentle curve of the anterior border of the symphysis is the same but E20928 retains LI_1 , LI_2 , RI_2 and RI_3 . Parts of both canines are preserved. In this specimen, LM_3 is intact, but only the trigonid of RM_3 remains. The rest of the tooth-bearing parts of the corpora are broken, but LP_4 and LM_2 , and RP_4 , RM_1 , and RM_2 have been restored to the specimen. The diastema in PQ2166 is shorter than those of the two Elandsfontein specimens, of which E20928 is the shorter, apparently because of its relatively large canine. The reconstruction of E20928 shows that the sum of the length of P_3 to M_2 was about the same as that in E16675 and in PQ2166. As the horizontal rami and the M_1 and M_2 are larger in the Elandsfontein specimens than in PQ2166, the implication is that the reduction of the premolars was even greater.

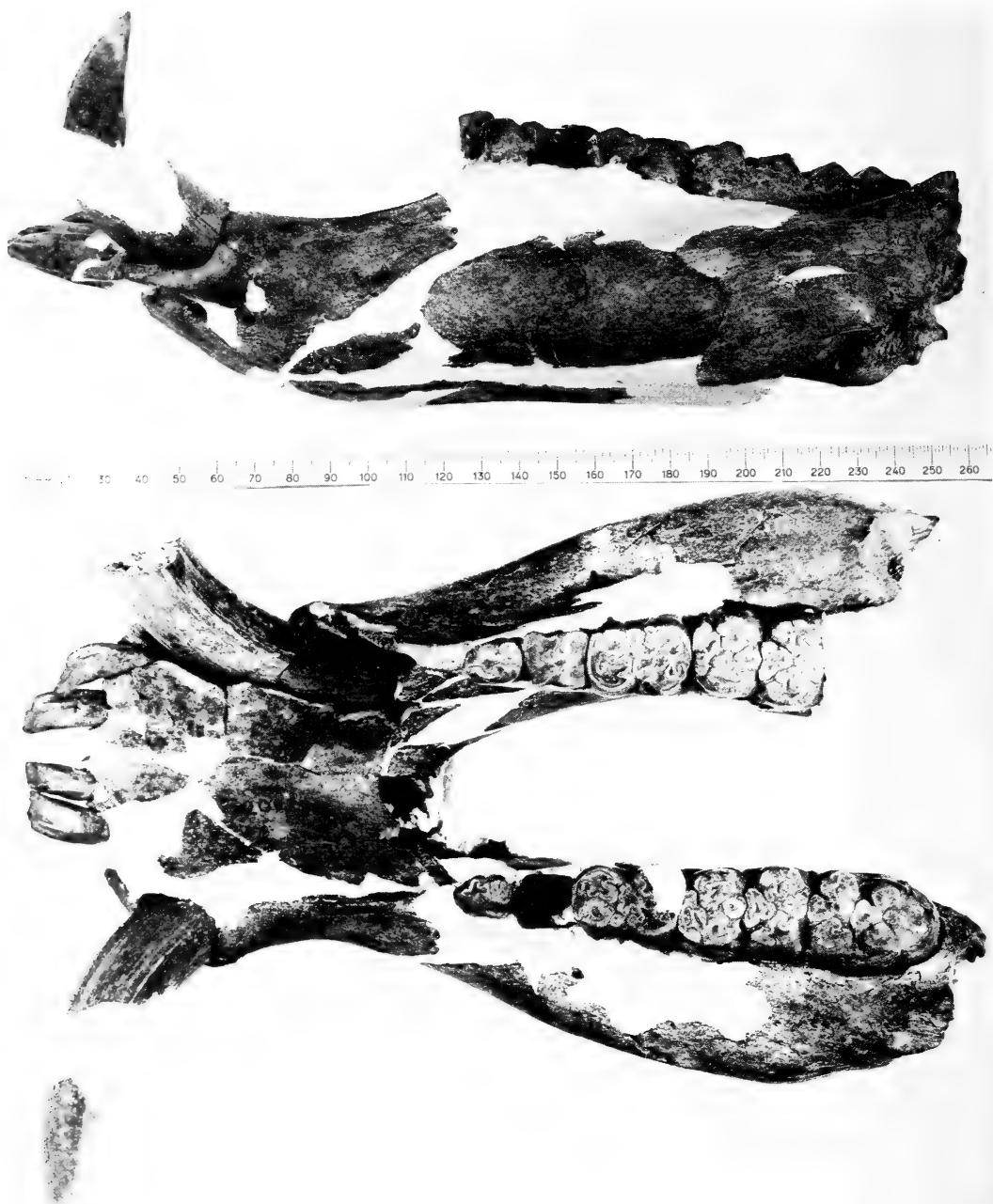


Fig. 13. Lateral and dorsal views of *Kolpochoerus paiceae* mandible from Elandsfontein (SAM-PQ-E20928).

The incisors are known only from the mandible E20928. They are essentially like those of the Skurwerug mandible although the RI_3 is a little wider.

The lower canines occur in the two symphyses, E16675 and 20928, although they are broken above the alveolar margin. In E16675 they are very similar in diameter to those in the Skurwerug mandible but they were clearly longer as the whole of the worn part of the tip is broken away and the remainder is more than 6 cm in length. In cross-section, they are almost heart-shaped or U-shaped, with a broad groove on the posterior face; this shape has been noted in female canines from Bed I, Olduvai. The roots are open but the pulp cavity is small, and the enamel is thin. In E20928 the cross-section is subtriangular with a faint keel caused by a shallow groove on the lateral (lingual) face. The lateral face has a length of 27 mm, the medial face 25 mm and the posterior 20,5 mm, as compared with 22, 21 and 18 mm respectively in the Skurwerug mandible and 21, 21 and 16 mm in E16675. There is no posterior groove and the roots are open in the normal fashion. The left canine of E20928 has been reconstructed and it extends about 10 cm from the alveolar margin, with a root length of at least 8 cm (Fig. 13). It is therefore appreciably longer than the canines of PQ2166, but much shorter than the canines of advanced *K. limnetes* males from East Africa. There are also two other specimens of the lower canine, E4019 and E7949. E4019 is part of a symphysis with 9 cm of the root area preserved; it is essentially similar to E20928. E7949 has lost the root area but the tip is preserved intact and shows a small anterior wear facet; the length is 14 cm as preserved and the cross-section resembles E20928.

In the only three specimens in which the relevant area is preserved, there is no sign of the possible presence of P_2 or of any scar to suggest its existence. Small roots for P_3 are seen in the symphysis E16675 and there is a P_3 socket in one of the specimens (ES17) described and figured by Singer & Keen (1955, pl. 22E, F). Judging from the alveolus, P_3 was even more reduced than that of PQ2166. The posterior root is very compressed, and its alveolus merges with that of P_4 . In addition to an apparent absolute size reduction in the ES17 P_3 compared with that of PQ2166, there is an even greater relative size difference, given the fact that ES17 represents a larger individual, with a molar row length of 123 mm against the 100 mm in PQ2166. Much the same applies in the case of E20928 since, although neither the P_3 nor its alveoli are preserved in this specimen, it is clear from the reconstruction that this tooth was as reduced as that of ES17 (Fig. 13).

The P_4 in the mandible fragment ES17 is slightly broken but the length is estimated as 15,5 mm and the breadth is 11,7 mm, fractionally larger than in PQ2166. There is a strong broad main pillar and a small posterior cusp, as in the Skurwerug jaw. The enamel is somewhat rugose. The best-preserved specimens in the Elandsfontein assemblage are an unequally worn pair associated with the mandible, E20928 (Fig. 13). The more worn right P_4 is morphologically very similar to those of PQ2166 but is slightly smaller. This is a further indication of the relatively greater reduction of the premolars in the Elandsfontein *K. paiceae*, since the mandible of E20928 is considerably more robust than that of PQ2166

(Table 3) and its M_3 is appreciably larger. The P_4 of E20928 is also distinct in having markedly rugose enamel, which is said by Harris & White (1979) to be an advanced character in East African *K. limnetes*.

There are five examples of M_1 . These teeth in E20928 and ES17 are in advanced wear (Fig. 13; Singer & Keen 1955, pl. 22E, F). In the latter the anterior and posterior pairs of pillars respectively are united into enamel-rimmed areas of dentine within which are small residual lakes of enamel; it is larger than the corresponding tooth in PQ2166. The LM_1 is present and unworn in the juvenile jaw fragment ES22 described and figured by Keen & Singer (1956, pl. 34) and in the original 'type' specimen ES5/6 (Singer & Keen 1955, pls 20, 21). M_1 is also present in two undescribed juveniles E5294 and E11859. The last named is also very similar in size to the teeth in PQ2166 but the other two are somewhat larger (Fig. 9). The morphology is normal.

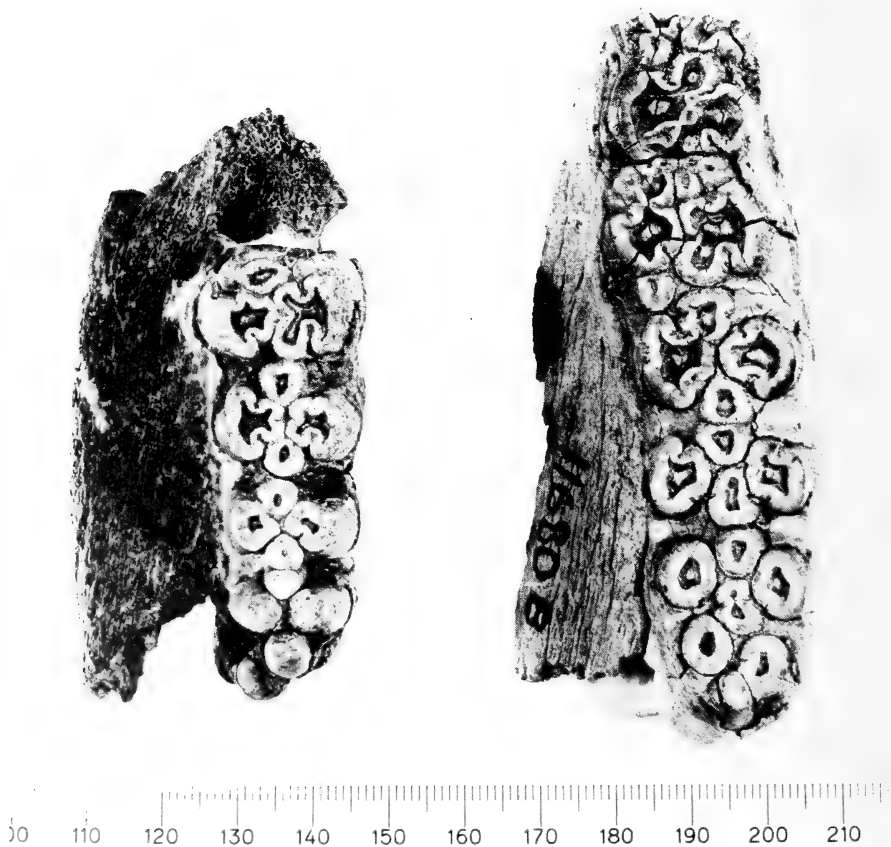


Fig. 14. Occlusal views of the smallest and largest lower third molars of *Kolpochoerus paiceae* from Elandsfontein (SAM-PQ-E3032 and E11680).

M₂ is present in ES17, ES3 and ES6 (Singer & Keen 1955, pls 20, 21, 22) and also, though damaged, in the two fragments of a mandible E11680 and in three other specimens, E20928 (Fig. 13), E20867 and E16910. ES3 is close in size to PQ2166 while the others are somewhat larger (Fig. 9). The morphology is normal for *Kolpochoerus*.

The lower M₃ is well represented in the Elandsfontein assemblage by 14 complete specimens belonging to 12 individuals as well as by several incomplete specimens. Half of these were described by Singer & Keen (1955) or by Keen & Singer (1956). The crown normally consists of four well-developed pairs of lateral pillars with a fifth pair weakly developed at or near the back of the crown. The two largest teeth, E11680A, B (Fig. 14), however, have only four paired laterals and two small terminal pillars that can hardly be termed a fifth pair. Most closely comparable with PQ2166 is the specimen ES28 (Keen & Singer 1956, pl. 33E). It was the only one to be selected by Keen & Singer (1956) for differentiation from '*Mesochorus lategani*' and placement in Broom's (1931) species '*M. paiceae*'. ES28 is indeed very similar to the M₃ of the type and of the 'neotype' from the Vaal River gravels (Shaw & Cooke 1941), although a little smaller. Both it and the smallest of the Elandsfontein third molars, E3032 (Fig. 14), are a little larger than the corresponding teeth in PQ2166 but are alike in pillar structure. Since the older fossils from Elandsfontein could represent more than one time interval, E3032 and ES28 may belong to an earlier temporal variant of *Kolpochoerus* at this locality. However, in view of the variation in detail in the number and arrangement of the minor elements at the back of the talonid that is normal in *Kolpochoerus* samples, the Elandsfontein sample can be regarded as a single species, so that '*M. lategani*' is a junior synonym of *K. paiceae*. The tallest unworn pillar (in E12822/11445) is 36 mm and it is the same in ES6 and ES16 (Singer & Keen 1955, pl. 20B). Thus the crown height of both upper and lower molars is generally greater than in most specimens from the upper parts of the Shungura and the Koobi Fora formations.

THE ZULULAND SPECIMEN

Fig. 15

During 1976, M. J. McCarthy of the University of Natal collected some fossils, including an incomplete *Kolpochoerus* tooth, from the Port Durnford Formation at Gabhagabha on the Zululand coast (McCarthy & Orr 1978).

This *Kolpochoerus* specimen (SAM-PQ2174) is a left M₃ in an early state of wear that lacks most of the anterior half of the trigonid (Fig. 15). The remaining part of the trigonid is similar in all observable respects to corresponding parts of the M₃ of PQ2166. The talonid also resembles that of PQ2166, as well as the smaller of the specimens from Elandsfontein. It is distinct in having a double median cusp anteriorly, a feature not observed in any other *K. paiceae* specimen. This is probably an individual or population characteristic that has no taxonomic significance. The talonid of PQ2174 lacks the small postero-lingual cusp present in



Fig. 15. Lateral and occlusal view of the *Kolpochoerus paiceae* lower third molar from the Port Durnford Formation, Zululand (SAM-PQ2174). Natural size.

PQ2166, a feature that accounts for the marginally greater talonid length in the latter (c. 29 mm as against 27 mm in PQ2174). The talonids of the smaller Elandsfontein specimens, and of the *K. paiceae* 'neotype' from the Vaal River gravels, are distinguished from that of PQ2174 principally by their slightly greater crown heights, which suggests that the Zululand specimen is in a more primitive evolutionary state. This specimen may therefore be like the one from Skurwerug in representing a somewhat earlier form of *K. paiceae*. Although the bases for comparison are limited, there is nothing that would preclude the Zululand and Skurwerug *K. paiceae* from being broadly contemporaneous.

DISCUSSION

The close similarity in size and morphology between the type M_3 of *Kolpochoerus paiceae* and the M_3 of the 'neotype', both of which came from the Vaal River gravels, leaves little doubt about their mutual identity. In the 'neotype' both P_3 and P_4 are smaller than in any of the East African material and very close in size to the Skurwerug specimen. The 'neotype' has a small pit in front of the P_3 that was interpreted as a root impression for P_2 , but as the M_3 in this specimen is not yet erupted, it is very possible that the anterior premolar would be shed in the adult. The M_3 in the Elandsfontein material covers a size range that includes both the type and the 'neotype' and this, coupled with the unusual reduction in the premolars, provides a sound basis for considering that all

represent the same species. The Skurwerug and Zululand specimens are distinct in having the M_3 slightly smaller than those in the other samples, but they are also identified with *K. paiceae*.

The Skurwerug skull is a good deal smaller than the 'advanced' female cranium from Peninj, although there are general resemblances, as may be expected in females of *Kolpochoerus*. In the Peninj cranium the occipital condyles are elevated well above the palatal plane but this is achieved by elevation of the whole occiput and braincase, as well as by increase of the height of the occiput itself as compared with 'typical' *K. limnetes*. In the Skurwerug cranium the condyles are also higher above the palatal plane than in 'typical' *K. limnetes*, but the occiput itself is shorter and the net result is that the braincase and orbits are not as elevated, although they may be higher than in the 'typical' form. Unfortunately, the braincase and occiput are not known in the best female cranium, KNM-ER 1085 from Koobi Fora, but in that specimen the rim of the orbit is lower than in the Skurwerug cranium. The reduction in size of the occiput in the Skurwerug cranium is unexpected and it is also notable that the paramastoid processes are not very robust. *Hylochoerus* also has elevated condyles and a short occiput but a different occipital morphology. Another point of difference between the Skurwerug cranium and that of the Koobi Fora female KNM-ER 1085 is that, far from the premolar reduction seen in PQ2166, the Koobi Fora female not only had normal-sized premolars but actually retained the P^1 18 mm in front of P^2 . The Peninj female on the other hand had lost P^2 but P^3 and P^4 were larger than normal. The Peninj female had kept the full complement of upper incisors as compared with the reduced complement in PQ2166. Thus the Skurwerug cranium shows a number of important features of difference from both the 'typical' and the 'advanced' *Kolpochoerus* of East Africa.

The two partial mandibles from Elandsfontein, E16675 and E20928, probably represent female and male individuals respectively, and they make it possible to reconstruct the mandible of 'typical' *K. paiceae* with some assurance. By comparison with mandibles of males of 'typical' *K. limnetes* from the Shungura Formation or the Koobi Fora Formation there are several striking features of difference. The corpus is unusually robust and expanded lateral to the second and third molars so that the overall width across the two horizontal rami is much greater than the width at the canine alveoli. The symphysis is unusually short, thus adding to the massive appearance of the jaw. The anterior border of the symphysis is flattened rather than arcuate, emphasizing the relative shortening and broadening of the jaw. The distance from the back of the canine to the front of the anterior premolar is about normal for *K. limnetes*, so the shortening is largely in the anterior part of the symphysis. The canines are stout but are more laterally directed and shorter than in 'typical' *K. limnetes*. While these features, apart from the premolar reduction, might be less striking in specimens from the lower part of the Shungura Formation (i.e. more than 2 Ma), they are very remarkable in the context of an age equivalent to the upper part of the Olduvai Beds (i.e. less than 1 Ma). The evolutionary trend in the 'advanced' *Kol-*

pochoerus from such levels is towards elongation of the jaw, especially of the symphysis, so that the distance from canine to anterior premolar is increased, as well as by forward arching of the incisor border. There is also a trend towards increased curvature and elongation of the canines. There is thus good reason to maintain the separateness of *K. paiceae*.

The Skurwerug mandible is less robust than the Elandsfontein specimens but the width across the two horizontal rami is substantially greater than the width across the canines. The symphysis is short and the incisive border flattened, as in the Elandsfontein material, and the somewhat phacochoerine profile of the symphysis is similar. Considered together with the premolar reduction, these features leave little doubt that the jaw belongs to the same species as the Elandsfontein material.

The lesser robustness of the Skurwerug mandible is consistent with the specimen representing a female, but the difference is greater than might be expected in a contemporary population, an opinion that would be confirmed if E16675 does indeed belong to a 'typical' *K. paiceae* female. It seems likely that the Skurwerug specimen represents an earlier, somewhat less specialized stock. This is borne out by the smaller size of the third molars, for in suids there is normally very little size difference in the cheek teeth of the two sexes. The upper third molars are very slightly larger than those in the Koobi Fora female KNM-ER 1085 which, however, have only three well-developed pairs of laterals whereas PQ2166 has an incipient fourth pair. The third molars from Olduvai Bed I and from the Shungura Member G likewise have three pairs of laterals in the uppers and four in the lowers, although additional posterior small pillars can occur. In size the third molars of the Skurwerug specimen are closely comparable with those from Member G of the Shungura Formation and with the sample from Bed I at Olduvai, both with ages close to 2 Ma. It would seem likely that *K. paiceae* diverged from a stock essentially at the 2–2,5 Ma level of development, strengthening rather than lengthening the talon (talonid) of the third molars while concurrently reducing the premolars and the upper incisors, molarizing the P⁴, shortening the symphysis, and increasing the robustness of the mandibular corpus, raising the level of the occipital condyles and reducing the height of the occiput itself. It seems reasonable to suggest that the Skurwerug skull retains more *K. limnetes*-like morphology than would be apparent in the later Elandsfontein sample, although the Skurwerug specimen is already clearly differentiated from its parent stock. It is therefore likely to date back between 1 and 2 Ma, and it seems desirable to allow about 0,5 million years for the continued specialization represented by the material from Elandsfontein. The bulk of the fossils from Elandsfontein have an age estimated as about 0,8 Ma (\pm 0,2 Ma) on the basis of correlation with Olduvai Beds III/IV.

Although not necessarily associated with PQ2166, the other fossils from Skurwerug are not inconsistent with this age estimate. The *Gazella* sp. is of some significance in suggesting a middle Pleistocene or older date, since this genus has not been recorded in younger faunas from the south-western Cape Province.

PALAEOENVIRONMENTAL IMPLICATIONS

Apart from its significance in terms of the history of the genus in South Africa, the Skurwerug *Kolpochoerus* specimen is remarkable in several other respects. Firstly, Suidae are a rare element in the Pleistocene faunas of the south-western Cape, and they were not present in this region at all during historic times. Even the large and diverse fossil assemblage from Elandsfontein includes relatively few suid specimens, with no more than a dozen *Kolpochoerus paiceae* and even fewer *Stylochoerus compactus* individuals having been recorded on the basis of very incomplete material. PQ2166 therefore stands out amongst the approximately 30 fragmentary fossils that make up the mammalian assemblage from Skurwerug. However, judging from other fossil occurrences in the vicinity of Saldanha Bay, it is likely that immense numbers of specimens were preserved in the Skurwerug dune, and it was only the scale and nature of the excavation and the restricted access to the site that prevented a more representative sample being collected. Thus, it is possible that the Skurwerug *K. paiceae* was as common an element in the fauna of its time as its counterpart from Elandsfontein.

The recovery of PQ2166 was clearly fortuitous, and was almost certainly due to the relatively large size and completeness of the specimen, which no doubt made it an obvious curiosity to the persons involved in its discovery and subsequent donation to the South African Museum. Indeed, it is the condition of the specimen that is perhaps its most remarkable feature. It is unquestionably the most complete suid specimen yet found in the Pleistocene deposits of the south-western Cape, and one of the best-preserved skulls of *Kolpochoerus* known anywhere. Many of the parts that are missing were lost after it had been excavated, and apparently only the left ascending ramus of the mandible was not preserved at all. The adjacent part of the left mandibular corpus shows signs of weathering on its lateral surface, suggesting that this area and the missing ascending ramus remained exposed after the rest of the skull had been rapidly buried and so preserved intact. Rapid burial was evidently the exception rather than the rule amongst recorded Pleistocene mammal fossils of the region. A high proportion of these specimens show signs of post-mortem damage caused by weathering and the activities of predators, scavengers and bone-gnawing animals such as the porcupine.

Since there is no record of the relationship between PQ2166 and the deposits in which it was incorporated, the taphonomy of this specimen cannot be determined with certainty. However, since the deposits represent a coastal dune, it is likely that the rapid burial of the specimen was effected by wind-blown sand. An implication of this is that the Skurwerug dune was still active at that time, and that PQ2166 therefore gives a direct indication of the age of the dune (i.e. early Pleistocene). It is, of course, also possible that the specimen became incorporated in the deposits after the dune had been stabilized through consolidation and a covering of vegetation. Solution cavities and small caves or burrows excavated by animals are features of consolidated calcareous dunes, and PQ2166 may have been deposited in such a feature. This could have resulted from the death of the

animal that had sheltered in such a cave or burrow, or as a result of the activities of another cave occupant. The latter alternative is unlikely, since the specimen shows no sign of the damage that characterizes the activities of man, hyaenas and porcupines, the only habitual cave-inhabiting bone-collectors that might have been involved in this instance. Even if PQ2166 does post-date the consolidation of the Skurwerug dune, it need not necessarily be much younger. The consolidation of local late Cenozoic calcareous dunes was often, or invariably, a relatively rapid process, so an early Pleistocene date for the one at Skurwerug could still apply. In spite of all these uncertainties, it is clear that the Skurwerug dune cannot post-date the *Kolpochoerus* specimen.

An early Pleistocene age for this dune is in accord with a recently published view on the relationship between late Cenozoic deposits and sea-level changes in the Saldanha region (Hendey 1981a, 1981b, 1983a). According to this interpretation of available evidence, the succession has not been affected by local tectonism and it reflects the global record of sea-level changes. That part of the record which is relevant here began during the early Pliocene when the sea rose to about 100 m above its present level, creating a channel linking Saldanha Bay to St. Helena Bay, with a large island forming its western margin and the mainland following a series of granite hills to the east (Hendey 1981b, fig. 5). This event represents the eustatic cycle TP1 of Vail *et al.* (1977), and is documented by the Varswater Formation, particularly the exposures in 'E' Quarry near Langebaanweg, where a rich fossil assemblage provides evidence of its age. During the middle and late Pliocene, sea-level fell and during this regressive phase there was a stillstand at about 50 m above present sea-level (cycle TP2). During a late Pliocene high-stand that was at about 20 m above present sea-level (cycle TP3 or Q1*), a 12 m submarine platform was developed at wave-base away from the shoreline in Saldanha Bay. This feature reflects the erosion that occurs in the upper 10–15 m of the marine environment (Flemming 1976). The platform is still visible inland from the north-eastern shore of Saldanha Bay, and is underlain by marine deposits that represent the Uyekraal Shelly Sand Member of the Bredasdorp Formation (Rogers 1983). The fluviatile deposits at Baard's Quarry near Langebaanweg are correlated with the 20 m high sea-level. The 12 m platform has evidently remained above sea-level since the regression that followed its formation. The Skurwerug dune is situated on the southern margin of this platform, which it overlies and clearly post-dates (Fig. 16). On the basis of this interpretation of local sea-level history during the late Tertiary, the Skurwerug dune must be of late Pliocene or younger age. The possible correlation of this dune with past sea-level changes may, however, be taken still further.

The actual elevation of the interface between the Skurwerug dune and the 12 m platform is not recorded, but judging from 1:10 000 orthophoto maps of the

*Q1 is a Quaternary cycle according to the definition of this period by Vail *et al.* (1977) and Beard *et al.* (1982), but it falls into the Pliocene if the Plio-Pleistocene boundary is taken at about 1.6 Ma (see Tauxe *et al.* 1983), the date which is accepted here. For the purposes of this study the early-middle Pleistocene boundary is taken at 700 ka and the middle-late Pleistocene boundary at 130 ka (see Butzer 1974).

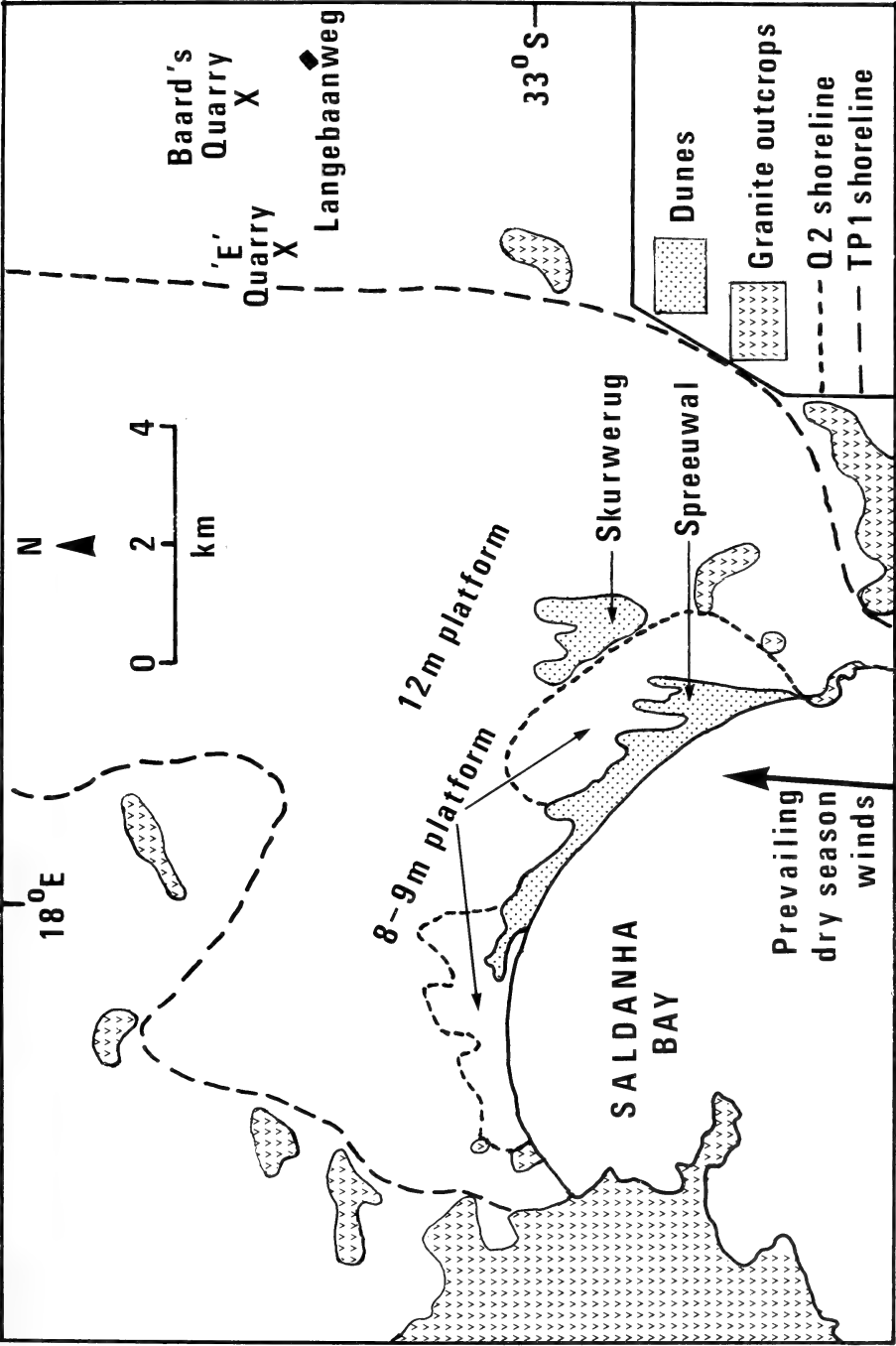


Fig. 16. Sketch-map of part of the Saldanha region showing localities and features referred to in the text. (Adapted from South African Geological Survey map 3217D & 3218C—St. Helena Bay, 3317B & 3318A—Saldanha Bay.)

area it must be in the order of 10 to 12 m. Between this dune and the Spreewal dune complex that fringes the present coastline is another platform, this one having an elevation of 8 to 9 m. It is here interpreted as a wave-cut platform that was developed in the intertidal zone during the high sea-level that existed when the Skurwerug dune itself fringed the coastline. Since this dune was situated on the coast and was probably no more than a few metres above sea-level, and since the 8 to 9 m platform has a veneer of aeolian sands, the actual elevation of the high sea-level concerned must have been at or a little below 8 m. There is in fact abundant evidence on the southern African west coast of a past high sea-level at about 7 to 8 m above present sea-level (e.g. Krige 1927; Mabbutt 1957; Hallam 1964; Carrington & Kensley 1969; Tankard 1976; Davies 1980). On the basis of the record of the *Kolpochoerus* specimen in the Skurwerug dune, this high sea-level is now dated as early Pleistocene.

Since this dating conflicts with most previously published opinions on the age of the 7–8 m high sea-level, the situation needs to be reviewed. Perhaps the most widely held opinion is that this high sea-level dates from the last (or Eemian) interglacial. For example, Davies (1980: 165) has stated that the Eem I (= oxygen isotope substage 5e) high sea-level at about 125 ka 'is widely accepted as around + 8 m over much of the world', and he cites local examples suggesting that this was also the case in at least some parts of southern Africa. However, in instances where evidence of age is available, that which indicates an Eemian age is equivocal, while that which indicates a pre-Eemian age is not. The evidence for selected areas or localities around the southern African coast is examined below.

Apart from the Skurwerug evidence, perhaps the most secure indication that the 7–8 m high sea-level on the southern African coast predates the last interglacial comes from the Port Durnford Formation on the Zululand coast (Hobday & Orme 1974). The mammalian fauna from near the base of this formation is clearly pre-Eemian, and is generally regarded as being of middle Pleistocene age (McCarthy & Orr 1978). The Port Durnford Formation *Kolpochoerus* tooth described above could be broadly contemporaneous with the Skurwerug *K. paiceae*, and the formation itself may therefore be earlier than has hitherto been supposed. There is in fact nothing in the Port Durnford fauna that precludes this possibility. The dating of this fauna had been based largely on an elephant, which has been identified as either *Loxodonta atlantica zulu* (Maglio 1973) or *Elephas zulu* (Beden 1983). According to Maglio (1973) it is essentially similar to the middle Pleistocene elephant from Elandsfontein. Elsewhere in Africa *L. atlantica* dates back beyond 2 Ma, so if the identification with this species is correct, then the Zululand elephant could be of pre-middle Pleistocene age. However, it is more likely that the material represents a species of *Elephas*, as indicated by Beden (1983). Since it is clearly less advanced than other middle Pleistocene representatives of this genus in southern Africa (e.g. *E. iolensis* from the Vaal River gravels and Victoria Falls), an early Pleistocene age for this elephant, and for the Port Durnford Formation, is probable.

The decision by Hobday & Orme (1974) to assign an Eemian date to the Port Durnford Formation appears to have been based largely on the artefact associations of this formation, and the mistaken belief that the Acheulian and Sangoan industries persisted well into the late Pleistocene. According to Hobday & Orme (1974), an Acheulian artefact was recovered from this formation, and if this was indeed the case, then it would be further evidence of a pre-Eemian age for the formation, since the Acheulian is no younger than about 150–200 ka anywhere in Africa (Volman 1984). In addition, a so-called 'Sangoan' handaxe was found on the surface of this formation, and although the age of the 'Natal Sangoan' or 'Tugela Industry' (Davies 1980) is not known, it is likely to be pre-Eemian. While there may be doubts about the nature and implications of the archaeological associations of the Port Durnford Formation, the faunal evidence is unequivocal in indicating a middle Pleistocene or earlier date for this formation. Judged on both sea-level evidence and the *Kolpochoerus* occurrences, it is very likely that this formation is an east-coast temporal equivalent of the Skurwerug dune.

At the same latitude as the Port Durnford Formation, but on the opposite side of the subcontinent near Oranjemund in South West Africa are deposits associated with a 7–8 m high sea-level that are termed the 'C Beach' or 'Main Terrace' (Hallam 1964: 701). The C Beach, like the Port Durnford Formation, has recently been dated as an Eemian interglacial feature (Anonymous 1982). This dating is unacceptable since Acheulian artefacts have been found overlying the C Beach (Davies 1980; Corvinus 1983). Corvinus (1983) concluded that the archaeological evidence indicates an age for this beach of between 400 and 700 ka although this dating is clearly tentative given the nature of the artefact association with the beach and the uncertainties surrounding the chronology of the Acheulian in Africa. Perhaps all that can be safely concluded from this evidence is that the C Beach is middle Pleistocene or older.

There are several records in the south-western and southern Cape Province of Middle Stone Age (MSA) artefacts associated with the 7–8 m high sea-level. Such occurrences have been used to conclude an Eemian interglacial or even younger age for this high sea-level. For example, this applies in the case of the open-air sites at Melkbos (Duinefontein) (Hendey 1968) and Bok Baai (Mabbutt *et al.* 1955), and the cave sites of Die Kelders 1 (Tankard & Schweitzer 1974) and Klasies River Mouth 1 (Butzer 1978). Vertebrate fossils and MSA artefacts were found at Duinefontein (see Fig. 1) in deposits that post-date a 6–8 m high sea-level (Hendey 1968). Although originally assigned to the last glacial period, it is now clear that these materials are much older and pre-date the Eemian interglacial, with the fauna indicating a 'later Middle Pleistocene' age (Klein 1976: 16). Early Stone Age (Acheulian) artefacts are also known from the area (Hendey 1974). The situation at Duinefontein is similar to that at Bok Baai, 12 km further north, where deposits overlying a 6–8 m beach contain both MSA and Acheulian artefacts (Mabbutt *et al.* 1955). In both these instances the 7–8 m high sea-level can be no younger than middle Pleistocene. The same applies at Cape Hangklip

(Fig. 1), where Acheulian artefacts 'extend to within 8 m of present sea-level' (Mabbutt 1957). The caves, Die Kelders 1 and Klasies River Mouth 1, were cut by a high sea-level of about 7–8 m and partly because the earliest recorded human habitation of these caves was during the MSA, this high sea-level was dated as Eemian. However, it was also admitted that in both these instances the caves could have been created before this interglacial, and then scoured by the highest of the Eemian transgressions (Tankard 1975; Butzer 1978).

The Eemian sea-level peak was reached during isotope substage 5e and was probably at about 4–5 m above the present level. This is the elevation of the B Beach at Oranjemund, which is associated with MSA artefacts (Corvinus 1983). Boulder ramparts and other features in the Saldanha Bay–Langebaan Lagoon area that indicate a high sea-level of up to 4,5 m were described by Parker (1968). Flemming (1980) gave a slightly lower estimate (3–4 m) for this high sea-level on the basis of wave erosion features and beach deposits on the Langebaan compound barrier, and suggested a mid-Holocene age for this event. It is here regarded as Eemian in age, although there is a beach ridge on this barrier 1 km east of Kreefbaai with a minimum elevation of 1,5 m (Flemming 1980) that evidently does represent a Holocene high sea-level. There is evidence that indicates that the age of events involved in the development of the Langebaan barrier were generally underestimated in earlier studies (e.g. Parker 1968; Birch 1976; Flemming 1977, 1980). The intertidal-flats deposits near Churchhaven contain vertebrate fossils that are middle Pleistocene or older. These fossils include undescribed elephant teeth that are in the collections of the South African Museum. They represent two extinct species. One is unidentified, but it may belong to a species that is of pre-middle Pleistocene age. The second is *Elephas iolensis*, an elephant that in southern Africa is known only from middle Pleistocene contexts. The deposits from which these specimens were derived overlie the core of the compound barrier, which Flemming (1977, fig. 22; 1980, fig. 51) incorrectly dated as 'late Pleistocene'. Clearly, the barrier can be no younger than middle Pleistocene, and it may in fact be even older. Consequently, the *circa* 4 m high sea-level that is reflected by deposits and features on the barrier need not be as young as Flemming and others have supposed.

The 7–8 m high sea-level has been dated as early Pleistocene on at least one previous occasion. This was done by Tankard (1976) on the basis of the record in the Saldanha region. Unfortunately, he based this dating on an incorrect correlation of the 7–8 m high sea-level in this region with the '45–50 m transgression complex' in Namaqualand, and on the mistaken assumption that the dating of this complex as 'Early Pleistocene' by Carrington & Kensley (1969) was correct. The former error arose from his unsubstantiated belief that the south-western Cape coast has been down-warped relative to that in Namaqualand, an opinion that was discounted by Hendey (1981a). A major objection to Tankard's (1976) correlation is that the 7–8 m high sea-level in the south-western Cape is associated with a cold-water molluscan fauna, whereas the fauna associated with the 45–50 m complex in Namaqualand includes warm-water elements. Tankard

explained this inconsistency by postulating lower sea temperatures in the Saldanha area. In fact, sea temperatures in the relatively shallow and enclosed Saldanha Bay are higher than those on the open Namaqualand coast, and there is no reason to suppose that the situation differed during the early Pleistocene. Although the basis for Tankard's dating of the 7–8 m high sea-level in the Saldanha region is unacceptable, it is perhaps significant that he recognized it to be of pre-Eemian age.

Another succession in the south-western Cape that has been correlated with the 7–8 m high sea-level is that at Swartklip on the False Bay coast (see Fig. 1). Barwis & Tankard (1983) have assigned an Eemian age to the Swartklip succession largely by inference. The only dateable element in this succession is a vertebrate fossil occurrence, which is probably of early last glacial age (Klein 1975). Since the fossils were accumulated in a small cave that was developed after consolidation of the deposits, they clearly post-date the sea-level events that led to the development of the Swartklip succession. The dating by Barwis & Tankard (1983) depended upon their acceptance of a late Pleistocene date for similar successions elsewhere on the South African coast, and their belief that these successions are contemporaneous with that at Swartklip. The other successions include the Port Durnford Formation, which was shown above to be of pre-late Pleistocene age. Presumably, its correlation with the Swartklip succession still applies, in which case the latter is also likely to be a temporal equivalent of the Skurwerug dune. A pre-Eemian date for the Swartklip succession also follows if it is accepted that the Spreeuwal and other dune plumes of the Cape west coast had their origins during the Eemian interglacial (see below). These plumes, which in part represent the Witsand Member of the Bredasdorp Formation, are younger than the consolidated deposits of the Swartklip succession and the Skurwerug dune, both of which are included in the Langebaan Limestone Member of this formation (Rogers 1983).

Two important points emerge from the preceding discussion. Firstly, since the late Cenozoic shorelines of the Saldanha region are unaffected by local tectonism, and since the 7–8 m shoreline is virtually ubiquitous on the southern African coast, it follows that this shoreline reflects a eustatic sea-level event. Secondly, this event represents a high sea-level stand that followed the one that peaked at about 20 m. The latter high sea-level has previously been dated as late Pliocene, with the opinion that it is more likely to date from the eustatic cycle Q1 than cycle TP3 (Hendey 1981*b*). If this is indeed the case, then the 7–8 m high sea-level is most likely to date from the subsequent cycle, Q2. According to Beard *et al.* (1982, fig. 1), the Q2 high sea-level stand occurred between 0.80 and 1.3 Ma, dates that are not inconsistent with the 1–2 Ma age estimate suggested for the Skurwerug *Kolpochoerus* on the basis of its evolutionary development. This fossil therefore dates from the latter part of the early Pleistocene, according to the subdivisions of this epoch accepted here (see footnote p. 44). The sea-level changes indicated by features and deposits in the Saldanha region are illustrated in Figure 17, and are summarized in Table 4.

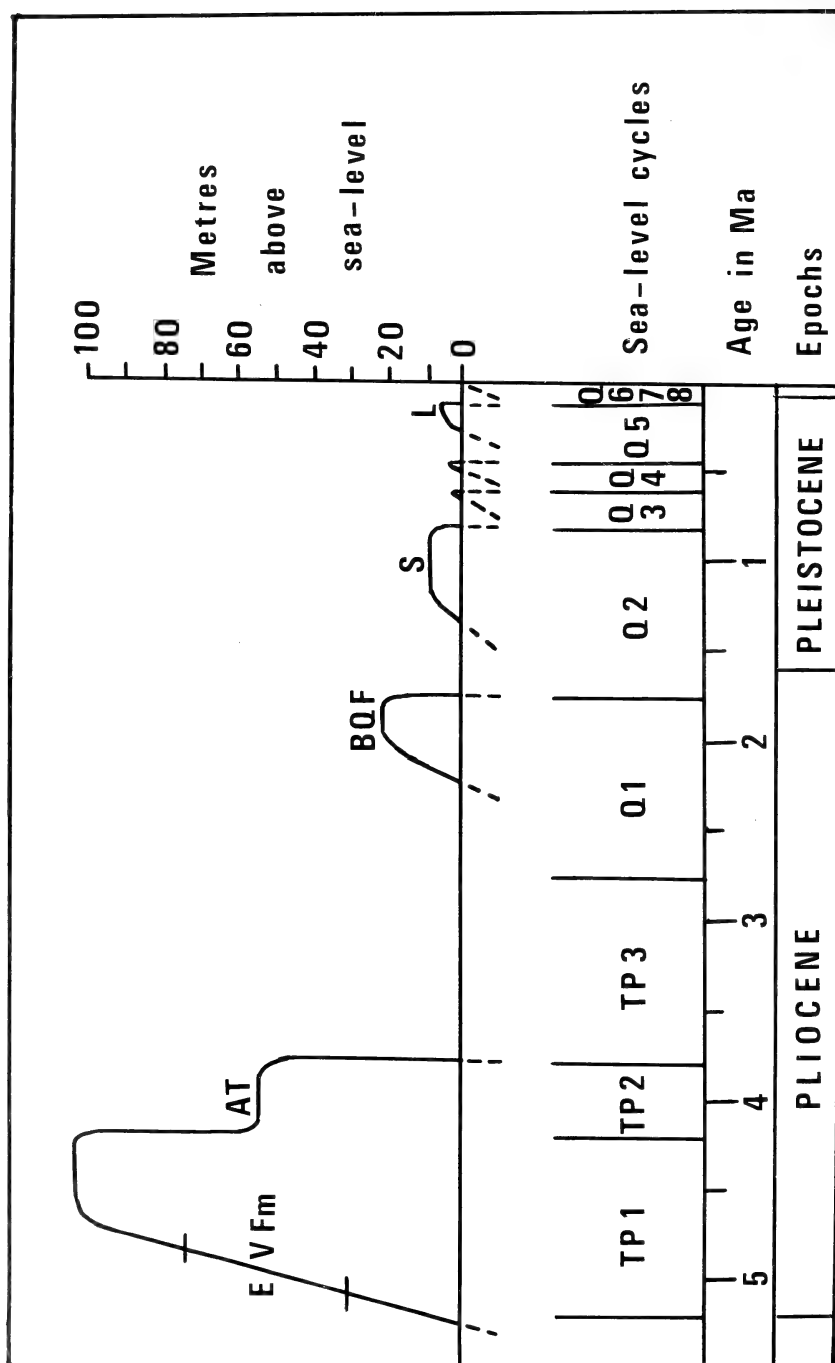


Fig. 17. Diagrammatic representation of sea-level changes indicated by features and deposits in the Saldanha region. (Adapted from Hendey 1981b, fig 4. EVFm-'E' Quarry, Varswater Formation; AT-Anyskop terrestrial deposits; BQF-Baard's Quarry fluvial deposits; S-Skurwerug dune; L-Langebaan barrier. Tertiary sea-level cycles after Vail *et al.* 1977; Quaternary cycles after Beard *et al.* 1982.)

TABLE 4
Pliocene to Holocene high sea-levels in the Saldanha region.

<i>Feature/deposit</i>	<i>Location</i>	<i>Height of sea above present level</i>	<i>Age</i>	<i>Eustatic cycle</i>
Beach ridge	1 km east of Kreefbaai	1,5 m	Holocene	Q8
Beach deposits and wave erosion features	Langebaan barrier	3–4 m	late Pleistocene (Eemian, 5e) 125 ka	Q5
Coastal dune and wave-cut platform	Skurwerug	7–8 m	early Pleistocene 0,8–1,3 Ma	Q2
Submarine platform	Inland from Skurwerug	c. 20 m	late Pliocene 1,75–2,05 Ma	Q1
Fluviatile deposits	Baard's Quarry, Langebaanweg			
Coastal dune	Anyskop, Langebaanweg	c. 50 m	middle Pliocene 3,8–4,2 Ma	TP2
Marine deposits	Groot Springfontein			
Erosion surfaces	Varswater, Witteklip, etc.			
Submarine platform (on Varswater Fm)	Elandsfontein	c. 100 m	early Pliocene 4,2–5,2 Ma	TP1
Paralic deposits (Varswater Fm)	'E' Quarry, Langebaanweg			

References: Pliocene—Hendey (1981a, 1981b); Late Pliocene/Holocene—this paper.

The Skurwerug *Kolpochoerus* and dune have other palaeoenvironmental implications. The dune itself is similar in some respects to the nearby Spreeuwal dune complex on the present shoreline of Saldanha Bay. The latter has been described by De la Cruz (1978) and it is similar to the series of 'dune plumes' on the Cape west coast discussed by Tankard & Rogers (1978), Rodrigues (1978) and Rogers (1982). It is a relatively small example of a dune plume and is situated adjacent to the beach on the north-eastern shore of Saldanha Bay. The Spreeuwal plume is not entirely unvegetated as indicated by Hendey (1983a, fig. 3), but consists of a complex of vegetated parabolic dunes, with 'hairpin' extensions inland that have a south to north orientation determined by the prevailing dry-season (summer) winds (Fig. 16). There are, however, some patches of unvegetated barchanoid dunes superimposed on the vegetated dunes. The largest

of the 'hairpin' dunes is the most easterly, and it has a maximum height of about 40 m and a length of a little over 2 km. The relatively small size of this plume is evidently due to the restricted sediment supply in Saldanha Bay, which is now unconnected with the only large river in the area (i.e. the Berg River, which discharges into St. Helena Bay). The largest of the west-coast plumes are situated north of river mouths, where fluvial sediments provide replenishment for the dunes (Tankard & Rogers 1978).

At least three phases of dune activity are evident in the dune plumes of the Cape west coast. The youngest dunes are active today and are clearly influenced by existing sea-level and climatic conditions. The dating of the two earlier phases of dune activity is by inference only. The partly vegetated dunes have been correlated with the Flandrian transgression (Rodrigues 1978), and regarded as the local equivalent of the 'Flandrian Episode I' dunes on the Californian coast (Cooper 1967), an area that is environmentally similar to the Cape west coast. The oldest dunes, which are completely vegetated, may be the local equivalent of the 'pre-Flandrian' dunes of California, and they may well date back to the highest of the sea-level stands during the Eemian interglacial (i.e. during oxygen isotope substage 5e).

The Skurwerug dune represents the vestiges of a dune plume that was apparently developed under similar circumstances during the 7–8 m high sea-level of the early Pleistocene. Judging from the remnants of this dune, its easterly parts at least must have been very like the easterly 'hairpin' dunes of the Spreewal plume in terms of orientation, height and length. This suggests that the climatic conditions that prevailed during the period of development of the Skurwerug dune (i.e. eustatic cycle Q2) must have been similar to those later in the Quaternary that influenced the formation of the Spreewal plume (i.e. cycles Q5 and Q8). Given the well-documented cyclicity of climates during the Quaternary, this is not unexpected, but the Skurwerug dune is significant in having provided the first direct evidence of the nature of early Pleistocene climate in the south-western Cape.

The similarity in the sizes of the Spreewal and Skurwerug dunes is also significant in suggesting that the sediment supply in Saldanha Bay was as restricted during the early Pleistocene as it was during the late Pleistocene and Holocene. It follows that the Berg River must already have been following its present course by the early Pleistocene, and that the last time it could have discharged into Saldanha Bay was during the 20 m stillstand of the late Pliocene (Hendey 1981a). The exclusively marine nature of the sediments that underlie the 12 m platform inland of Saldanha Bay (Rogers 1983) is a further indication that the Berg River had diverted to a more northerly course by the end of the Pliocene.

It has already been indicated elsewhere that the Skurwerug *Kolpochoerus*, and the other mammals recorded from this locality, provide evidence that the local vegetation in their lifetimes differed from that of the present (Hendey 1983b). Although the habitat preference of *Kolpochoerus* cannot be precisely defined, this genus is likely to have inhabited fairly densely vegetated areas, since

its dentition is more like those of the living forest hog and bushpig than that of the open-country warthog. The present strandveld and fynbos vegetation communities of the Saldanha region are clearly unsuitable habitats for Suidae, and it is likely that at least some forested or wooded patches still existed in this region during the early Pleistocene. Furthermore, even though they may not have been contemporaries of the *Kolpochoerus*, the grazers represented in the Skurwerug deposits (i.e. *Equus*, *Connochaetes*, *Gazella*) support the view that grasses were more prominent in the Pleistocene vegetation communities of the south-western Cape than is the case today (Hendey 1983b). The present vegetation communities of the Cape west coast are clearly not a prerequisite for the formation of the coastal dune plumes.

To sum up, the discovery of the Skurwerug *Kolpochoerus paiceae* skull was a fortunate event for a variety of reasons. Not only has this fine specimen shed further light on the history of *Kolpochoerus* in South Africa, it has also resulted in further support for the correlation of the west-coast late Cenozoic succession with global sea-level changes. In addition, by indicating the likely age of the Skurwerug dune, it has led to the conclusion that local climatic conditions during the early Pleistocene were at least in some respects similar to those later in the Quaternary. Finally, it adds to the growing body of evidence that Pleistocene vegetation communities of the south-western Cape coastal plain were generally very different from those of the present.

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- WHITE, T. D. & HARRIS, J. M. 1977. Suid evolution and correlation of African hominid localities. *Science* **198** (4312): 13–21.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

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semicolon separates more than one reference by the same author

full stop separates references by different authors

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dash, not comma, separates consecutive numbers.

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Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Capital initial letters

- The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...': '... in *C. namacolus* (Fig. 10) ...'
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e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
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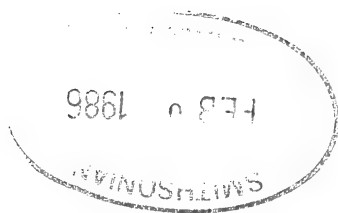
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(MAMMALIA, SUIDAE) FROM SKURWERUG,
NEAR SALDANHA, SOUTH AFRICA, AND ITS
PALAEOENVIRONMENTAL IMPLICATIONS

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ANNALS

OF THE SOUTH AFRICAN
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1. MATERIAL should be original and not published elsewhere, in whole or in part.

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FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* 74 (33): 627–634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) 2 (17): 309–320.

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THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* 4 (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* 16: 269–270.

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ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

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EARLY PLIOCENE IBISES
(AVES, PLATALEIDAE)
FROM SOUTH-WESTERN CAPE PROVINCE,
SOUTH AFRICA

By
STORRS L. OLSON

Cape Town Kaapstad

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EARLY PLIOCENE IBISES (AVES, PLATALEIDAE)
FROM SOUTH-WESTERN CAPE PROVINCE, SOUTH AFRICA

By

STORRS L. OLSON

*National Museum of Natural History, Smithsonian Institution,
Washington, D.C.**

(With 5 figures and 2 tables)

[MS accepted 15 July 1985]

ABSTRACT

Two species of ibises (Plataleidae) are recognized in the early Pliocene avifauna from Langebaanweg, south-western Cape Province, South Africa. One of these, *Geronticus apelex* sp. nov., is described from a partial associated skeleton and a few other referred specimens. *Geronticus apelex* was smaller than extant members of the genus and was more similar in morphology to the Palearctic species *G. eremita* than to the South African species *G. calvus*. A single end of a tibiotarsus is referred to the genus *Threskiornis* and is indistinguishable from the living species *T. aethiopicus*. These reports constitute the first Tertiary record for either genus. The living species of *Geronticus* characteristically inhabit dry, open areas and are not paludicolous. The South African species, *G. calvus*, is dependent upon short vegetation maintained by fires and grazing by ungulates for optimum foraging habitat. These ecological requirements would have been met in the early Pliocene at Langebaanweg, when the environment was becoming increasingly arid and where periodic fires and abundant ungulates are known to have been present.

CONTENTS

	PAGE
Introduction	57
Systematics	58
Discussion	68
Acknowledgements	68
References	69

INTRODUCTION

In the extensive collections of fossil birds from the early Pliocene Varswater Formation at Langebaanweg (Rich 1980; Hendey 1981) are remains of two species of ibises (Plataleidae). The present study describes these specimens and completes the analysis of all the fossils recovered thus far from Langebaanweg that are referable to the traditional order Ciconiiformes, which, however, is an unnatural, polyphyletic assemblage (Olson 1979, 1984, 1985). Other ciconiiform families known from Langebaanweg are the Scopidae (hamerkops), with one species, *Scopus xenopus* Olson (1984), and Ciconiidae (storks), with a single new

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species of *Ciconia* (P. Haarhoff MS). Herons (Ardeidae), flamingos (Phoenicopteridae), and shoe-bills (Balaenicipitidae) are absent in these deposits, despite the fact that flamingos and herons are common in the Cape region today.

The fossils treated here are housed in the collections of the Department of Cenozoic Palaeontology at the South African Museum, Cape Town; all fossil specimen numbers are prefixed by the acronym SAM-PQ, which has been omitted below. Other museum acronyms are explained in the acknowledgements.

Comparative material examined

Skeletal material of most species of ibises is scarce. The majority of the more critical species needed for this study were represented largely or entirely by a few unsexed captive birds. The specimens examined were as follows: *Geronticus eremita* IRSB 2057, IRSB 7459, IRSB 41072, MVZ 155199; *G. calvus* TM 33348, TM 33434, TM 60076; *Pseudibis papillosa* IRSB 64593; *Bostrychia hagedash* UMMZ 158551, UMMZ 214345, USNM 322594; *B. carunculata* AMNH 3894; *Lophotibis cristata* AMNH 3788; *Threskiornis aethiopicus* USNM 558412, USNM 558413, USNM 558415, USNM 558416; *T. melanocephalus* USNM 347314; *T. spinicollis* USNM 347785; *Nipponia nippon* USNM 16687; *Mesimbrinibis cayennensis* USNM 345762, USNM 345763; *Theristicus caudatus* USNM 227359, USNM 345764; *T. branickii* USNM 10022; *Harpiprion caerulescens* USNM 227358; *Cercibis oxycerca* DMNH 58261; *Phimosus infuscatus* UMMZ 158609, UMMZ 158610, UMMZ 218530; *Eudocimus albus* USNM 19787, USNM 500882; *Plegadis falcinellus* USNM 430823, USNM 502162, USNM 502696, USNM 502698; *P. chihi* USNM 498686; *P. ridgwayi* USNM 502127; *Platalea alba* USNM 558417.

SYSTEMATICS

Family Plataleidae

Any consideration of the systematics of ibises is hampered by the lack of a modern generic revision of the family grounded in internal anatomy. In examining the skeletons of most of the extant genera of Plataleidae, it became apparent that osteological differences between genera are not particularly profound. Nor are the more distinctive characters distributed in a manner that consistently allows genera to be clustered meaningfully. Preliminary observations nevertheless suggest that departures from the generic classification of Steinbacher (1979) will eventually prove necessary. Although only a single pathological captive specimen of *Pseudibis papillosa* was available for examination, no trenchant characters by which *Pseudibis* could be separated from *Geronticus* were detected. No skeleton of the giant ibis *Thaumatibis gigantea* was available for this study; however, it would be premature to follow Holyoak (1970) in including this distinctive species in the genus *Pseudibis* without anatomical confirmation.

Genus *Geronticus* Wagler, 1832

The fossil species described below is referable to the genus *Geronticus* by the combination of (1) narrow, tapering premaxilla and mandibular symphysis, lacking an expanded tip; (2) fairly shallow, curved mandibular rami; (3) retro-articular processes of the mandible not strongly developed; (4) rostrum deep, particularly the ventral bars; (5) narrow, elongate cranium; (6) short, robust tarsometatarsi; and (7) proportionately very long wing elements.

This combination of characters is not met with in any other genus, with the possible exception of *Pseudibis*. Among African genera of ibises, *Threskiornis* and *Plegadis* have the bill markedly expanded at the tip and have much longer tarsometatarsi, particularly in *Plegadis*. *Geronticus* and *Bostrychia* are similar in sharing short tarsometatarsi and a narrow bill tip, but in *Bostrychia* the retroarticular processes of the mandible are much better developed than in the fossil species.

Geronticus apelex sp. nov.

Figs 1-5

Material

Holotype. L20692, partial associated skeleton including the following elements: 37 mm section of premaxilla including the anterior portion of the internal (ventral) narial opening; much of the cranium (partially reconstructed) including frontals, occiput, and auditory regions; portions of the mandible including 30 mm of the tip, the proximal third of the right and the left dentary, and the right articular region; half of a pterygoid; atlas; axis; right forelimb including most of the humerus (partially reconstructed), ulna lacking part of the area around the brachial depression, radius, radiale, and carpometacarpus lacking part of the minor metacarpal; right hindlimb including femur, tibiotarsus lacking distal third, and tarsometatarsus; and various small fragments, mostly cranial. The specimen is from the Quartzose Sand Member (QSM) of the Varswater Formation at Langebaanweg, Cape Province, South Africa.

Paratypes. L13052W2, left coracoid (QSM); L28174M, scapular two-thirds of right coracoid (QSM); L4236D, scapular half of left coracoid (Pelletal Phosphorite Member (PPM), bed 3aS); L20755K, left scapula lacking posterior fourth (QSM). Including the holotype, the minimum number of individuals is two.

Measurements of holotype (in mm)

Cranium: width at point of articulation of nasal bars, 16,8; width through auditory region, 23,3; estimated length from point of articulation of nasal bar to posterior margin of occiput, 44. Mandible: length as reconstructed, 150; width at a point 20 mm caudad from tip, 3,2; antero-posterior diameter of articular surface, 7,0; medio-lateral diameter of articular surface, 8,0; least depth through articulation, 6,7. Atlas: depth, 7,4. Axis: width, 11,3. Humerus: length, 111,4;

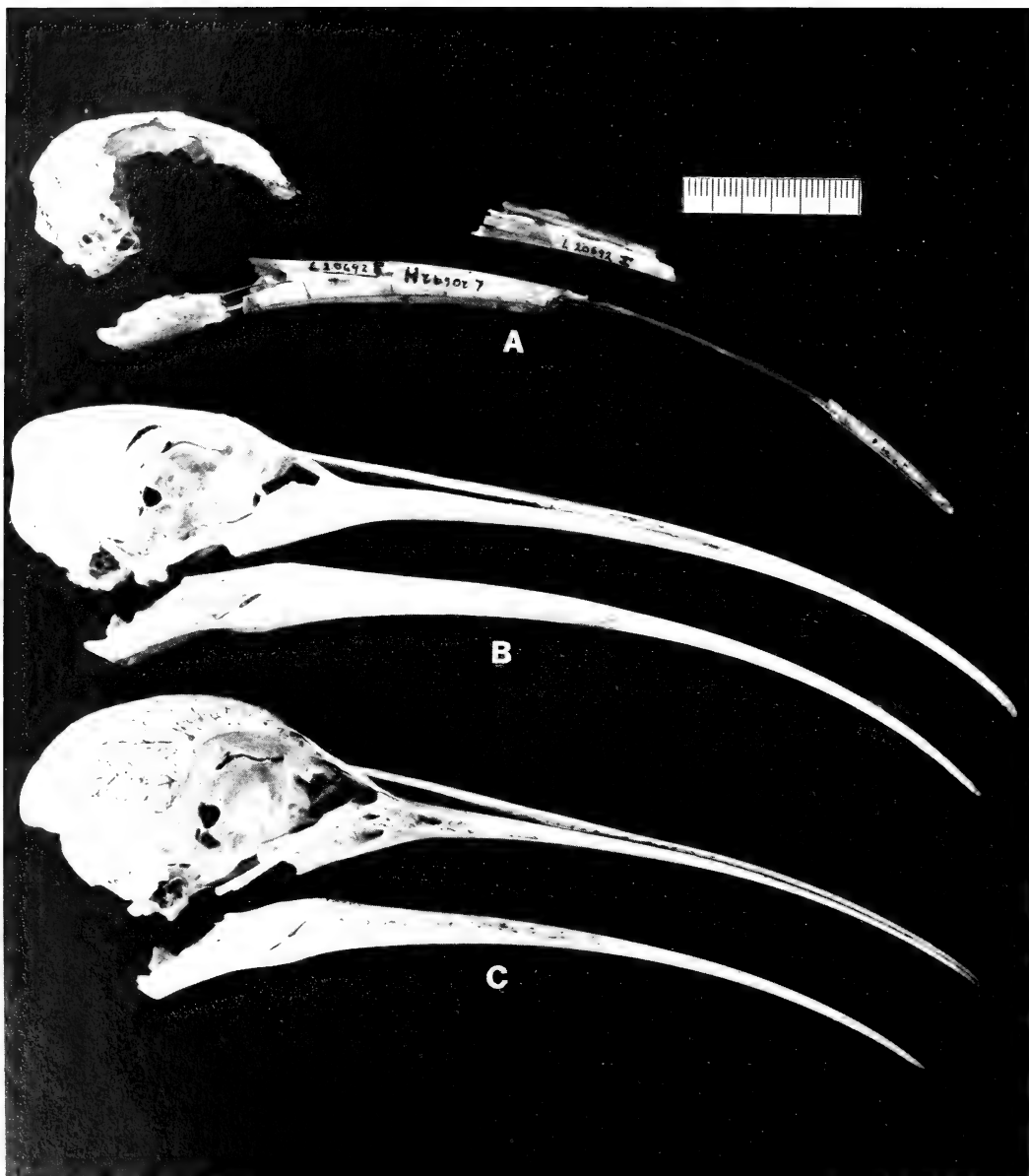


Fig. 1. Right lateral view of skulls and mandibles of *Geronticus*. A. *G. apex* sp. nov., holotype, SAM-PQ-L20692. B. *G. eremita*, MVZ 155199. C. *G. calvus*, TM 33348. The occipital crest in *G. eremita* may be better developed in presumably older individuals but never approaches the condition in *G. calvus*. Scale is in mm.

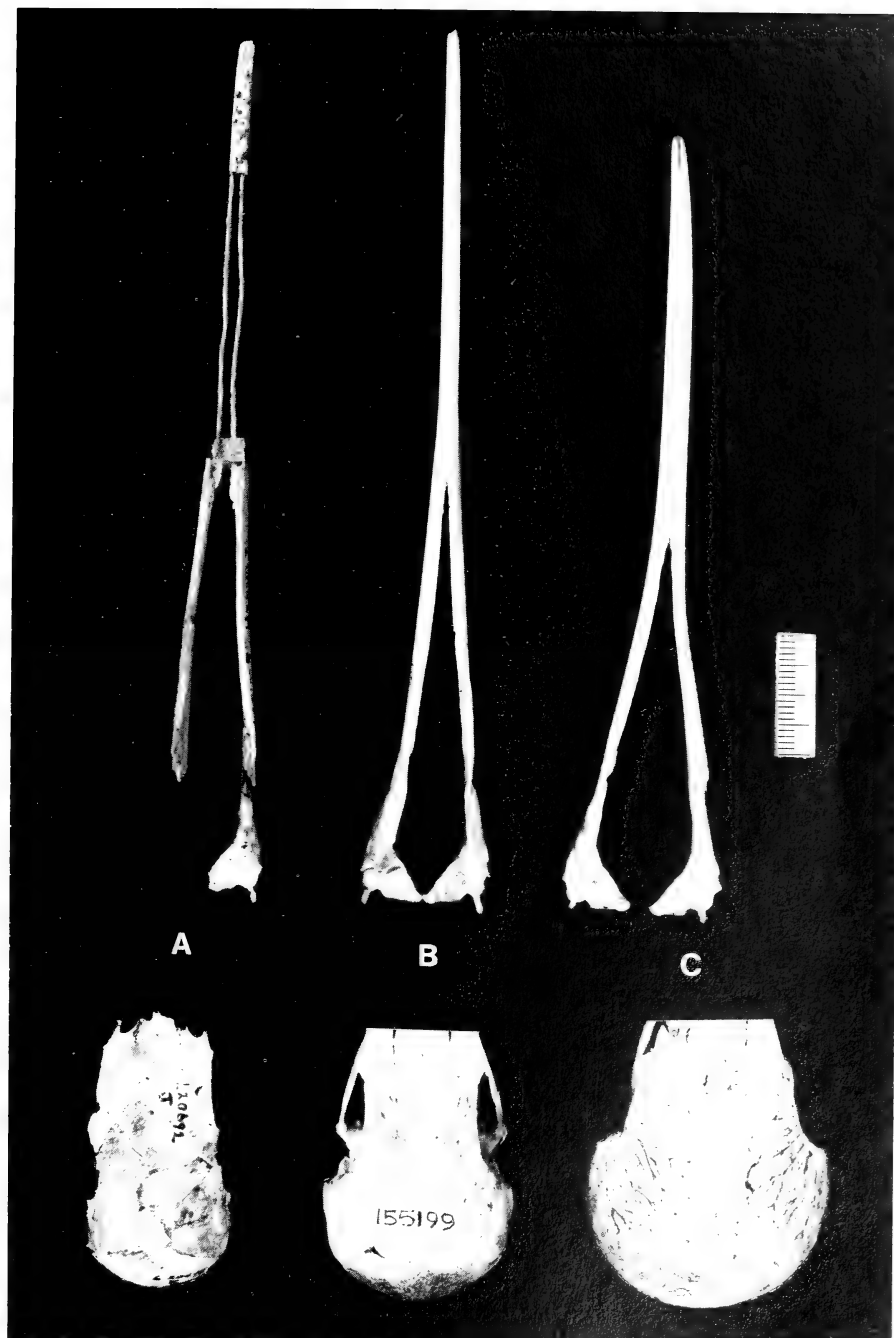


Fig. 2. Dorsal view of mandibles (top row) and crania (bottom row) of *Geronticus*.
 A. *G. apex* sp. nov., holotype, SAM-PQ-L20692. B. *G. eremita*, MVZ 155199.
 C. *G. calvus*, TM 33348. The cranium of *G. apex* is partly reconstructed and is lacking portions along the lateral margins that would make it slightly wider. Scale is in mm.

shaft width at narrowest point, 8,4; shaft width at proximal limit of brachial impression, 12,4; greatest diameter of brachial impression, 9,0; distal width, approximately 18,5; length of dorsal condyle, 7,6. Ulna: length, 122,5; proximal width and depth, $13,3 \times 9,0$; width and depth of shaft at midpoint, $5,5 \times 6,1$; distal width and depth, $7,8 \times 9,7$. Radius: length, 116,4; greatest proximal diameter, 6,7; least and greatest diameter of shaft at midpoint, $3,2 \times 4,6$; greatest distal diameter, 8,9. Carpometacarpus: length, 60,8; depth through alular metacarpal, 13,4; proximal width through trochleae, 6,0; width and depth of major metacarpal at midpoint, $5,0 \times 3,9$; greatest distal diameter, 9,2. Femur: length, 57,4; proximal width, 12,5; depth of head, 5,2; width and depth of shaft at midpoint, $5,5 \times 4,9$; distal width, 12,7; depth through medial condyle, 8,8; depth through lateral condyle, 10,3. Tibiotarsus: proximal width through articulation, 10,1; length of fibular crest, 17,1; width and depth of shaft at approximate midpoint, $5,2 \times 4,3$. Tarsometatarsus: length, 64,6; proximal width, 11,6; depth through hypotarsus, 10,9; width and depth of shaft at midpoint, $4,9 \times 3,8$; distal width, 11,7; width and depth of middle trochlea, $4,5 \times 5,9$.

TABLE 1

Length measurements (mm) of major elements of *Geronticus apelex* sp. nov. compared with extant species of *Geronticus* and *Pseudibis* (means in parentheses).

	<i>G. apelex</i> (n = 1)	<i>G. eremita</i> (n = 4)	<i>G. calvus</i> (n = 3)	<i>P. papillosa</i> (n = 1)
Coracoid	40,4	45,4–47,2 (46,1)	45,7–47,0 (46,1)	—
Humerus	111,4	126,3–130,0 (128,6)	117,6–124,1 (119,9)	—
Ulna	122,5	139,6–145,3 (142,5)	128,0–137,5 (131,8)	138,9
Carpometacarpus	60,8	71,0–72,9 (71,9)	64,4–69,8 (66,8)	71,5
Femur	57,4	64,8–66,7 (65,8)	65,5–69,9 (67,2)	64,7
Tarsometatarsus	64,6	72,9–74,6 (73,7)	69,1–77,2 (72,2)	81,5

Measurements of paratypes (in mm)

Coracoid, L13052W2: length from head to medial angle of sternal articulation, 40,4; length and width of glenoid facet, $10,3 \times 5,8$. Coracoid, L28174M: length and width of glenoid facet, $10,5 \times 6,3$. Coracoid, L24236D: length and width of glenoid facet, $10,8 \times 6,2$. Scapula, L20755K: greatest diameter of anterior end, 9,7.

Diagnosis

Smaller than either of the extant species of *Geronticus* (or *Pseudibis*) (Table 1). Cranium rather narrow and elongate, lacking any of the occipital expansion into a crest as seen in the two living forms (greatly exaggerated in *G. calvus*, in which the top of the cranium is monstrously inflated both laterally

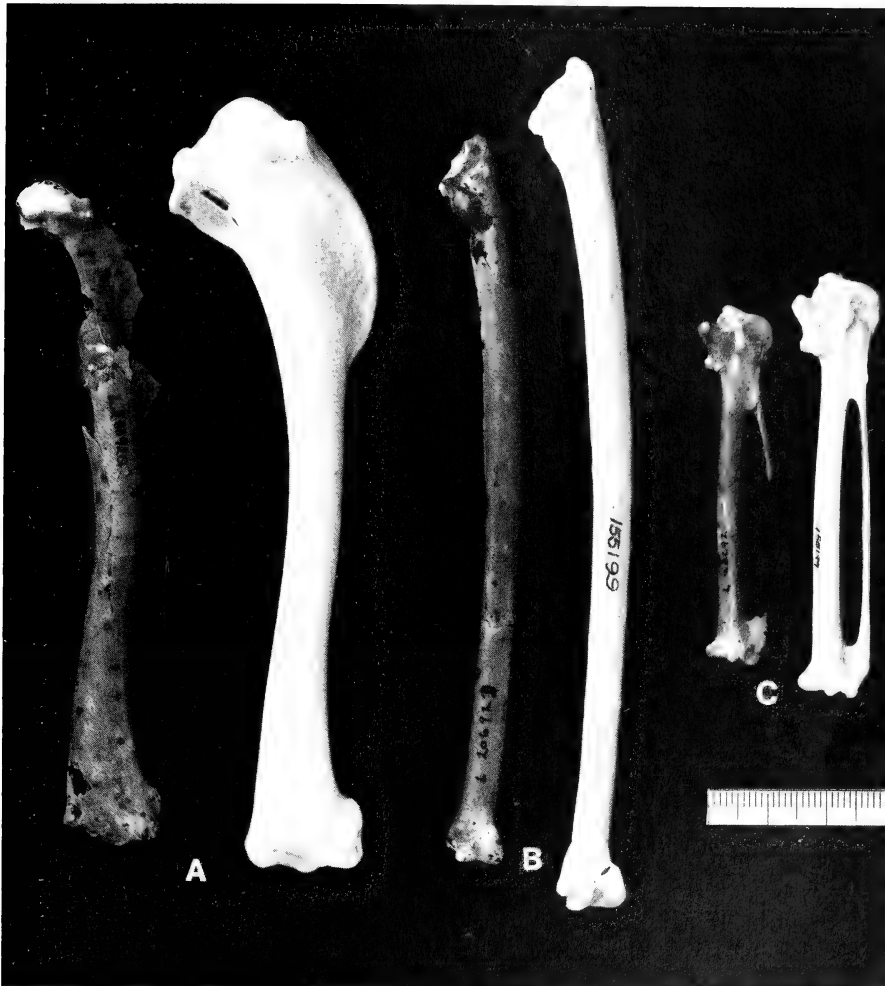


Fig. 3. Wing elements of *Geronticus apelex* sp. nov., holotype, SAM-PQ-L20692 (on left in each pair) and *G. eremita*, MVZ 155199. A. Humeri. B. Ulnae. C. Carpometacarpi. Scale is in mm.

and posteriorly). Mandibular symphysis narrow as in *G. eremita*, not broader and more flattened as in *G. calvus*. Compared to modern species of *Geronticus*, the procoracoid foramen of the coracoid is smaller, the brachial depression of the humerus is smaller, not extending as far proximally, with the brachial depression of the ulna being correspondingly small; the trochanter of the femur in lateral view is more proximally extended into a point, appearing narrower and less truncate. The wing elements are proportionately longer than in *G. calvus*, being more similar to those of *G. eremita*.



Fig. 4. Hindlimb elements of *Geronticus apex* sp. nov., holotype, SAM-PQ-L20692 (on left in each pair) and *G. eremita*, MVZ 155199. A. Femora. B. Tibiotarsi. C. Tarsometatarsi. Scale is in mm.

As mentioned above, *Pseudibis* is very similar to, and possibly congeneric with, *Geronticus*. In the one poor skeleton of *P. papillosa* examined, the distal foramen of the tarsometatarsus was more proximally situated than in *G. apex* or in any of the modern specimens of *Geronticus*.

Distribution

Early Pliocene Varswater Formation (Quartzose Sand Member and Pelletal Phosphorite Member bed 3aN) at Langebaanweg, south-western Cape Province, South Africa.

Etymology

Greek, *a-*, without, and *pelex*, helmet, in reference to the lack of an expanded bony occipital crest such as found in modern species of *Geronticus*. The name is a feminine noun in apposition.

Remarks

The specimens of *Geronticus apelex* provide the only Tertiary record for the genus.

The paratypical coracoids and scapula agree with a species the size of the holotype of *G. apelex*. The referred coracoids differ from *Plegadis* in having the sternal articulation convex rather than concave, from *Threskiornis* in not having the area of muscular attachment on the dorso-sternal surface markedly excavated, and from *Platalea* in lacking the distinct, wide, flat clavicular articulation. The coracoids are distinctive in having the procoracoid process expanded posteriorly and medially, giving the shaft a very robust appearance. In this respect the coracoids also differ from *Plegadis* and *Threskiornis* and more closely resemble *Geronticus* and *Bostrychia*. However, there appears to be considerable intra- and interspecific variation in the development of the procoracoid process in *Geronticus* and *Bostrychia*.

The wing elements seem disproportionately long in the holotype of *Geronticus apelex* and this is confirmed by computing the ratio of the length of the long bones to femur length (Table 2). Dividing by the length of the most

TABLE 2

Ratios of lengths of some long bones of African ibises divided by femur length. All ratios for *Geronticus apelex* are computed from the holotype. Except for one male of *G. eremita*, all the specimens of *Geronticus* and *Bostrychia* were unsexed. In *Threskiornis* and *Plegadis*, measurements are for two males and two females each; in *Plegadis* there is considerable sexual dimorphism in the size of the tarsometatarsus, which is proportionately much longer in males.

	Humerus	Ulna	Carpometacarpus	Tarsometatarsus
<i>Geronticus apelex</i> sp. nov. (n = 1)	1,94	2,13	1,06	1,12
<i>Geronticus eremita</i> (n = 4)	1,93–1,98	2,14–2,22	1,07–1,11	1,10–1,14
<i>Geronticus calvus</i> (n = 3)	1,77–1,80	1,93–1,98	0,97–1,01	1,05–1,10
<i>Bostrychia hagedash</i> (n = 3)	1,78–1,82	2,05–2,10	0,99–1,02	1,11–1,24
<i>Bostrychia carunculata</i> (n = 1)	1,79	2,05	0,98	1,04
<i>Threskiornis aethiopicus</i> (n = 4)	1,66–1,69	1,91–1,95	0,94–0,97	1,33–1,41
<i>Plegadis falcinellus</i> (n = 4)	1,59–1,68	1,69–1,91	0,95–0,99	1,52–1,78

complete paratypical coracoid yielded practically identical results. By either standard, *G. apelex* has a relatively longer humerus, ulna, and carpometacarpus than any of the species compared except *G. eremita*. The relative shortness of the tarsometatarsus in *Geronticus*, as compared to *Threskiornis* and *Plegadis*, is also demonstrated.

The greater similarity in the proportions of the wing of *G. apelex* to those of *G. eremita*, as opposed to *G. calvus*, may reflect migratory or nomadic propensities in the fossil species. *G. eremita* migrates well out of its breeding area in the autumn and early winter, whereas *G. calvus* is more sedentary. In lacking the great occipital expansion of *G. calvus*, the fossil species is likewise more similar to *G. eremita*, in which the occipital crest is much less developed. Within *Geronticus*, the lack of an expanded occipital crest would almost certainly be primitive, as such a crest occurs nowhere else in the family. The narrower and less flattened mandible of *G. apelex* is also more similar to that of *G. eremita* than *G. calvus*.

The ranges of *G. eremita* and *G. calvus* are now widely separated, with the former having occurred historically in Europe, the Middle East, and in northern Africa, although it is now reduced to two breeding populations, one in Turkey and the other in Morocco (Smith 1970). *Geronticus calvus* is restricted to South Africa, being found in mountainous areas from southern Transvaal to north-eastern Cape Province, having formerly extended to the south-western Cape (Siegfried 1966). The two species of *Geronticus* are now commonly regarded as forming a 'superspecies' (e.g. Snow 1978). The superspecies concept has become

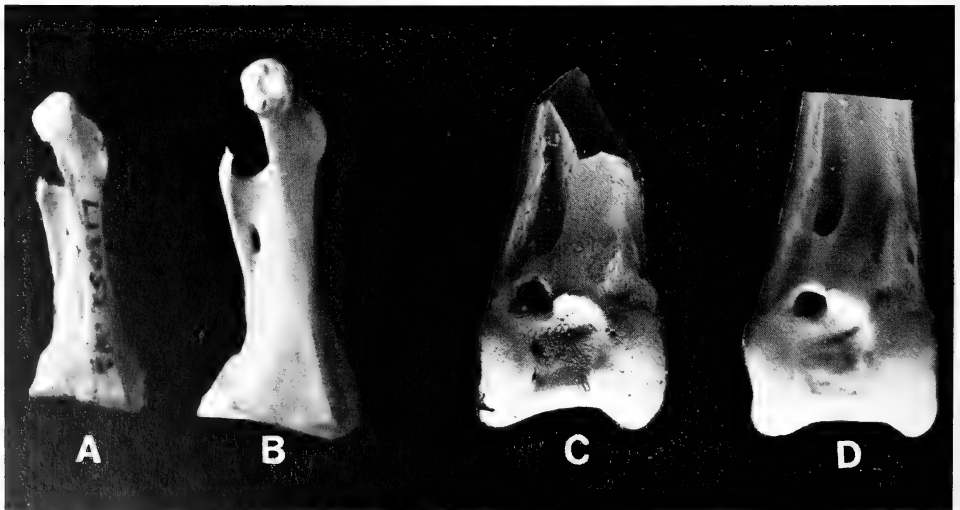


Fig. 5. Left coracoids of *Geronticus* (A-B) and distal ends of left tibiotarsi of *Threskiornis* (C-D). A. *G. apelex*, sp. nov., paratype, SAM-PQ-L13052W2. B. *G. calvus*, TM 33434. C. *T. aff. aethiopicus*, SAM-PQ-L28479G. D. *T. aethiopicus*, USNM 558413.

A and B, natural size; C and D, twice natural size.

very fashionable in recent years but through constant abuse and misapplication (e.g. American Ornithologists' Union 1983) has lost whatever utility it may once have had. In the case of *Geronticus*, it is doubtful that the superspecies category is appropriate. The differences between the two living species, at least in skull morphology, are considerable and it is possible that their ancestors may have existed sympatrically, particularly if one of them were smaller in size, as is *G. apelex*. The great differences in cranial adornment may perhaps have evolved as specific isolating mechanisms at a time when the two species were formerly in contact. Taking this view, *G. apelex* could be regarded as a smaller ancestral form of *G. eremita*, to which it is most similar.

With the available evidence, however, there is no satisfactory basis for deciding whether *G. apelex* represents (a) an extinct lineage that was contemporary with the ancestors of *G. eremita* and *G. calvus* and that left no descendants, (b) the primitive direct ancestor of one or the other of the two living species, or (c) the primitive sister group of both *G. eremita* and *G. calvus* that gave rise to both forms subsequently. The last seems the least likely, however, in view of the geologically young age of the Langebaanweg deposits and of the fact that modern species lineages were already clearly established in other groups of birds in the same deposits.

Genus *Threskiornis* Gray, 1842

Threskiornis aff. *aethiopicus* (Latham, 1790)

Fig. 5C

Material

Distal end of left tibiotarsus L28479G.

Distribution

Early Pliocene Varswater Formation (QSM) at Langebaanweg, southwestern Cape Province, South Africa.

Measurements

The distal width of this specimen is 13,1 mm, which is very near the mean for this measurement in the living species *Threskiornis aethiopicus* (12,1–14,4 mm, mean 13,2 mm, $n = 8$).

Remarks

This specimen is larger than in modern African species of ibises except *T. aethiopicus*, and differs further from *Geronticus* and *Bostrychia* in the much more prominent tubercle above the intercondylar fossa, this being almost lacking in *Geronticus* and only slightly better developed in *Bostrychia*. It is much too large and robust for *Plegadis*. Compared to *Platalea* it is relatively stouter, the intercondylar fossa is shallower and wider, and the distal end in distal view is not

nearly as elongated antero-posteriorly. This specimen cannot be distinguished from *T. aethiopicus*. It provides the only Tertiary record for the genus *Threskiornis*.

DISCUSSION

Although ibises are usually considered to be closely associated with marshes and fresh water, the modern relatives of the two species found in the Langebaanweg deposits are not restricted to such habitats. In fact, *Geronticus apelex* probably indicates quite different conditions, because both the modern species of *Geronticus* characteristically inhabit open, arid areas or grasslands. Both are also gregarious and nest in regions with rocky escarpments. Such outcrops occur in the Piketberg massif, some 50 km from Langebaanweg. Because *G. apelex* may have been migratory or nomadic, it need not have bred close to the site of deposition.

The living species *Geronticus eremita* is found 'most often on dry wadi beds, rocky slopes or semi-desert' (Cramp 1977: 344). *Geronticus calvus* frequents open grasslands and forages extensively in burnt areas, resorting to heavily grazed grasslands and pastures outside of the burning season (Manry 1981, 1985a, 1985b). Before the onset of human disturbance, Manry (1981) considered that suitable habitat for *G. calvus* would have been maintained by lightning-caused fires and grazing by native ungulates, particularly the black wildebeest, *Connochaetes gnou*.

The habitat requirements of *Geronticus* in general, and of *G. calvus* in particular, fit very well with the palaeoecological conditions inferred at the time of deposition of the Varswater Formation at Langebaanweg, when the environment was becoming drier and cooler and the vegetation was giving way to open grassland and fynbos (Hendey 1981). There is considerable evidence not only for the presence of numerous ungulates but for the existence of lightning-caused fires as well (Hendey 1981). Thus, the ecological conditions at Langebaanweg in the early Pliocene would seem to have been ideal for a species of *Geronticus*.

Threskiornis aethiopicus is usually associated with water, particularly areas of fresh-water marsh, which may be a prerequisite for breeding. However, in the Cape region today it is also found along the coast and is commonly seen foraging in open, arid pasturelands far from any body of water (McLachlan & Liversidge 1978), for which reason little palaeoecological significance attaches to the presence of a single individual of *Threskiornis* in the Langebaanweg deposits.

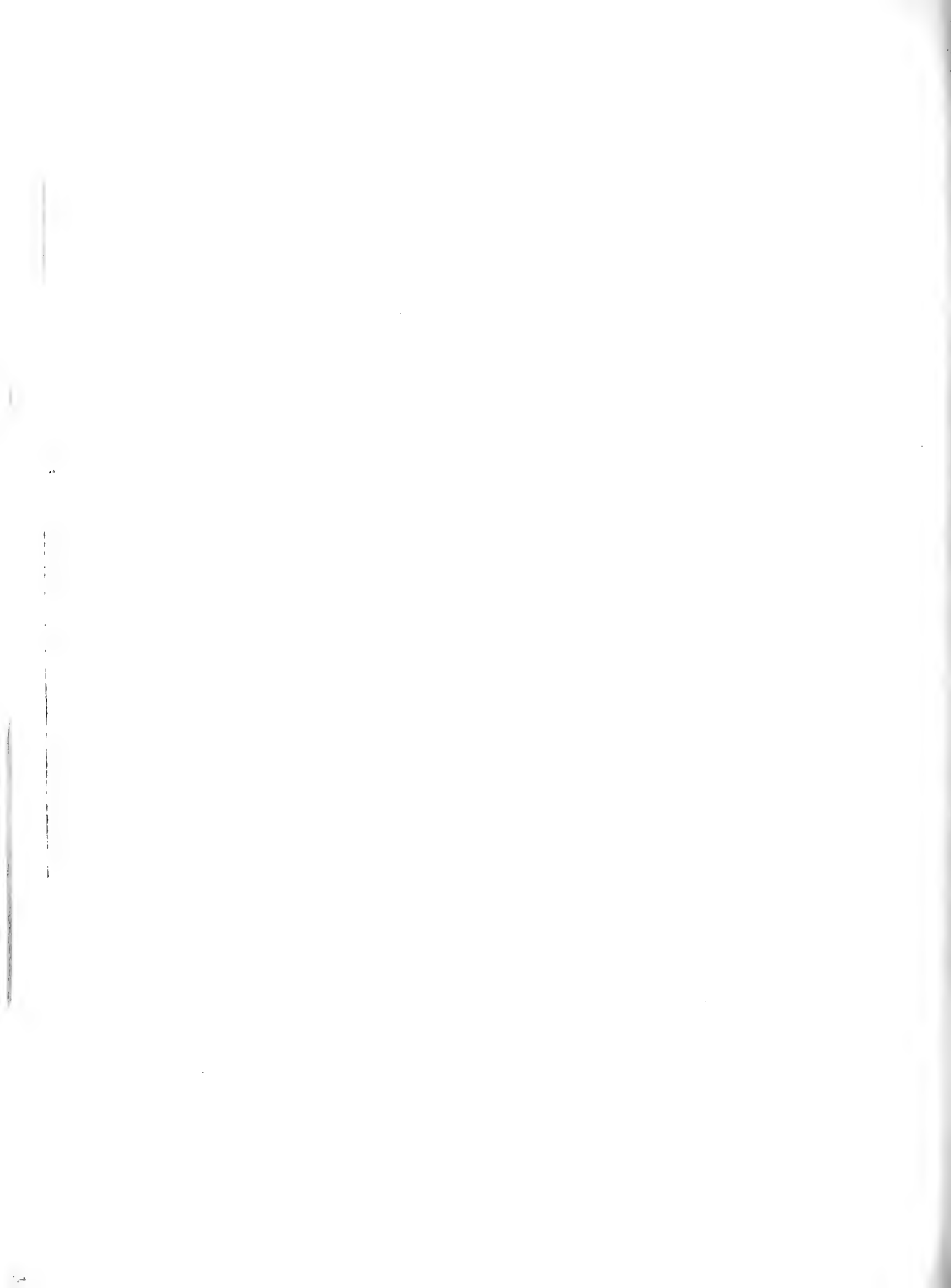
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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

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STORRS L. OLSON

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(AVES, PLATALEIDAE)
FROM SOUTH-WESTERN CAPE PROVINCE,
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A TAXONOMIC REVIEW OF THE
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FRASER-BRUNNER, 1949
(MYCTOPHIDAE, OSTEICHTHYES)

By
P. ALEXANDER HULLEY

Cape Town

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A TAXONOMIC REVIEW OF THE LANTERNFISH GENUS
TRIPHOTURUS FRASER-BRUNNER, 1949
(MYCTOPHIDAE, OSTEICHTHYES)

By

P. ALEXANDER HULLEY

Department of Marine Biology, South African Museum, Cape Town

(With 8 figures and 3 tables)

[MS accepted 1 November 1985]

ABSTRACT

The genus *Triphoturus* includes two known species: *Triphoturus nigrescens* (Brauer, 1904) and *Triphoturus mexicanus* (Gilbert, 1890). For the latter species, a southern population and a northern population may be distinguished on the basis of gill-raker counts. Phenotypic variation in serial meristic data may be environmentally induced in the northern population, accounting for differences between specimens from the California Current region and from the Gulf of California. The two species are described, together with comments on their distributions, including the first records of *Triphoturus nigrescens* in the Atlantic Ocean; here this species possesses an Agulhas Subpattern of distribution. A lectotype (ZMB 17617) is designated for *Myctophum (Lampanyctus) nigrescens* Brauer, 1904.

CONTENTS

	PAGE
Introduction	71
Methods	72
Results	73
Discussion	76
Systematic account	84
Acknowledgements	91
References	92

INTRODUCTION

The subgenus *Triphoturus* was created by Fraser-Brunner (1949) to include five species: *Lampanyctus microchir* Gilbert, 1913; *Myctophum (Lampanyctus) micropteron* Brauer, 1906 (with *Myctophum oculum* Garman, 1899, being considered a junior synonym); *Myctophum (Lampanyctus) nigrescens* Brauer, 1904; *Serpa turneri* Fowler, 1934; and *Myctophum mexicanum* Gilbert, 1890. On the basis of osteological and photophore evidence, Paxton (1972) raised the status to that of a genus, phylogenetically closely related to *Lampanyctus* Bonaparte, 1840, but distinguished from it by the possession of five VO photophores and by the presence of a small dorsal process on the opercular head of the hyomandibular. Later, in his list of nominal genera and species, Paxton (1979) included two

definite species, *Myctophum mexicanum* Gilbert (with the questionable junior synonym *Myctophum oculeum*) and *Myctophum (Lampanyctus) nigrescens* (with the questionable junior synonym *Lampanyctus microchir*), and one possible species (*Myctophum (Lampanyctus) micropterus*), within the genus *Triphoturus*.

However, the taxonomic status of the species of the genus is still unresolved (Hulley 1984). The type-series of *Myctophum (Lampanyctus) micropterus* Brauer, 1904, comprises two species (Hulley 1981): *Lampanyctus isaacsi* Wisner, 1974 (ZMB 17614, 17615—Gulf of Guinea) and *Triphoturus micropterus* (Brauer, 1906) (ZMB 17616—east of Seychelles), with the latter specimen designated as the lectotype for the purposes of stability. Further, no differences between this lectotype and the descriptions of *Triphoturus microchir* (Gilbert) given by Gilbert (1913) and Nafpaktitis & Nafpaktitis (1969) were observed, so that *Triphoturus microchir* was synonymized with *Triphoturus micropterus* (Hulley 1981). On the other hand, Wisner (1976) synonymized *Triphoturus microchir* (Gilbert) with *Triphoturus nigrescens* (Brauer, 1904), as there appeared to be no differences warranting the retention of Gilbert's species.

Brewer (1973) and Wisner (1976) suggested, not only on the basis of numbers of vertebrae and gill rakers but also on the distinctiveness of the larvae (Moser & Ahlstrom 1970; Ahlstrom 1971), that *Triphoturus mexicanus* is a species-complex consisting of two species: a 'southern' species referable to *Triphoturus oculeus* (Garman), and a 'northern' species referable to *Triphoturus mexicanus* (Gilbert). Further, Wisner (1976) stated that the latter species consists of two probable, but as yet unnamed, subspecies—one occurring in the Gulf of California from 30°N to 18°N, and the other in oceanic waters of the California Current between 38°N and 20°N, with a southern extension to 13°N in the region of 127°W. A similar distinction was drawn by Robison (1972) on the basis of higher relative abundance values in the Gulf of California. For the *Triphoturus mexicanus*-complex Imsand (1982, figs 22, 23, 25) differentiated: (1) a Gulf of California population from a California Current population (both termed *Triphoturus mexicanus*) on the criterion of occurring in areas south and east of 23°N 111°W; and (2) a southern population (termed *Triphoturus oculeus*) from the two northern populations, on the criterion of occurring south of 16°N. She stated, however, that these populations are allopatric, with very few areas where individuals of the two populations can be captured in the same net tow (Imsand 1982, fig. 26).

The purpose of the present paper is to clarify the species composition of the genus *Triphoturus* by the examination of the types and other material.

METHODS

The material examined is listed separately under each species in the Systematic Account. The species are listed alphabetically and type localities are given in parentheses in the synonymies. Methods for taking measurements and counts follow Nafpaktitis (1973). A total of 13 morphometric measurements,

each to the nearest 0.1 mm, were made on each specimen with needle-point callipers and using a binocular dissecting microscope where necessary. These include: SL—standard length; HL—head length; HD—head depth; BD—body depth; UJ—upper jaw length; ED—eye diameter; CPL—caudal peduncle length; CPD—caudal peduncle depth; PreD—predorsal length; PreAd—preadipose length; PreP—prepectoral length; PreV—preventral length; PreA—preanal length. A total of six meristic counts were made on each specimen, including: D—dorsal rays; A—anal rays; AOa—AOa photophores (left and right); AOp—AOp photophores (left and right); [AOt = AOa + AOp]; GRu—gill rakers on upper limb (left); GRl—gill rakers on lower limb (left); [GRt = GRu + 1 + GRl].

Photophore groupings are in accordance with Paxton (1972) and their abbreviations are given by Hulley (1981). The following additional abbreviations are used in reference to material examined:

CAS — California Academy of Sciences, San Francisco, USA

LACM — Los Angeles County Museum of Natural History, Los Angeles, USA

MCZ — Museum of Comparative Zoology, Harvard, USA

SAM — South African Museum, Cape Town, RSA

SU — Stanford University Natural History Museum, Stanford, USA
(specimens now housed in CAS)

USNM — National Museum of Natural History, Washington DC, USA

ZMB — Zoologisches Museum, Berlin, GDR

Statistical analyses and scatter plots were performed on an Apple IIe computer using STATPRO (Wadsworth Electronic Publishing Company) and standard reference texts (Snedecor & Cochran 1967; Sokal & Rohlf 1969; Zar 1974). Computer programmes for analysing morphometric data to allow for size-free comparisons of shape among specimens (Humphries *et al.* 1981; Johnson & Feltes 1984) were not available to the author. Meristic data were plotted according to the method of Hubbs & Hubbs (1953).

RESULTS

Where possible, morphometric data (in mm) and meristic data for the type specimens are given in Table 1. These specimens and the additional material have been divided into five groups for the purposes of analysis, with the number of specimens given in parentheses:

Group A. California Current region: meristics—CAS 24312 (30), LACM 39201–1 (48), SAM–24926 (3); morphometrics—CAS 24312 (30).

Group B. Gulf of California: meristics and morphometrics—SU 68 (2), SU 46808 (30).

Group C. Middle American Trench: meristics—LACM 31125–27 (27).

Group D. Central and eastern South Pacific: meristics—LACM 33603–18 (3), LACM 33676–7 (4), LACM 33696–11 (4), MCZ 28500 (3), MCZ 35185 (1),

TABLE 1
Triphoturus. Measurements (in mm) and counts of examined type specimens.

Species	Status	No. of specimens	Catalogue No.	SL	HL CPD D	HD PreD A	BD PreAd AOa	UJ PreP AOp	ED PreV GRu	CPL PreA GRI
<i>M. mexicanum</i>	lectotype	1	USNM 76343	42,8	—	—	—	—	—	8,6
				—	21,6	—	—	—	—	—
	paralectotypes	2	SU 68	52,5	16,1	8,8	9,6	10,4	3,7	12,1
				—	4,1	25,4	39,9	15,7	22,0	30,0
				—	13	15	—	—	4	13
<i>M. oculateum</i>	syntypes	3	MCZ 28500	50,4	15,3	8,6	9,0	10,7	4,0	10,9
				—	4,1	24,4	38,6	16,1	22,8	30,3
				—	13	16	4	6	4	12
				58,4	16,8	9,1	10,4	11,8	5,0	—
				—	4,9	28,2	45,6	—	—	34,4
	syntypes	1	MCZ 35185	—	13	—	—	—	3	10
				28,6	8,9	5,2	5,4	6,4	1,9	5,7
				—	2,0	15,1	22,2	9,4	13,2	16,9
				—	—	15	—	—	3	10
				(37) [#]	—	—	—	—	—	—
	syntype	1	MCZ 35185	—	—	—	—	—	—	—
				—	—	—	—	—	—	—
				—	—	6	—	3	10	—
	syntype	1	MCZ 35187	54,9	15,4	8,5	9,0	11,4	4,1	—
				—	4,2	27,8	44,1	16,7	23,7	33,7
				—	13	15	5	—	3	11
<i>L. microchir</i>	holotype	1	USNM 74468	44,0	13,0	7,4	7,9	8,3	2,9	9,0
				—	3,6	21,8	34,7	12,7	18,6	26,8
				—	12	16	5	5	4	10
<i>M. micropterum</i>	syntype†	1	ZMB 17614	17,0	5,1	3,2	3,1	4,0	0,8	4,0
				—	1,1	9,3	13,4	5,6	—	9,4
	syntype†	1	ZMB 17615	—	(14)	(17)	4	6	3	8
				74,7	18,1	11,0	11,3	14,5	3,8	16,1
	syntype†	1	ZMB 17615	—	6,3	33,9	55,0	21,1	28,5	38,9
				—	15	17	6	7	5	13
	syntype*	1	ZMB 17616	21,0	—	—	—	—	—	—
				—	—	—	—	—	—	—
	syntype*	1	ZMB 17616	—	—	—	—	—	—	—
				—	—	—	—	—	—	—
<i>M. nigrescens</i>	syntype	1	ZMB 17617	18,2	—	—	—	—	—	—
				—	—	—	—	—	—	—
				—	15	16	5	6	3	8
	syntype [#]	1	ZMB 22379	29,3	—	5,0	5,0	6,1	1,9	—
				—	1,8	16,6	23,1	9,2	13,6	17,4
				(10)	14	—	4	6	3	8

†—*Lampanyctus isaaci* Wisner, 1974 (*fide* Hulley 1981)

*—lectotype of *M. micropterum*—*fide* Hulley (1981)

[#]—specimen dried out or damaged

TABLE 2

Triphoturus. Morphometrics: standard length (SL) in millimetres; all other distances expressed as percentages of SL.

	n	SL	HL	HD	BD	UJ	ED	CPL	CPD	PreD	PreAd	PreP	PreV	PreA
Group A	30	39,5–62,0	28–35	14–18	15–19	19–23	6–8	20–24	7–10	47–53	74–88	28–36	40–47	56–66
Group B	30	22,7–59,7	30–33	17–19	18–20	20–23	6–9	19–22	8–10	47–51	74–81	30–34	40–46	57–63
Group D	11	28,6–69,0	25–32	14–18	16–19	17–22	6–8	19–23	7–9	46–53	75–81	26–33	39–46	57–63
Group E	20	13,1–33,4	27–31	13–17	12–17	18–23	5–7	19–25	5–7	50–55	76–81	28–33	42–45	55–61

MCZ 35187 (1), MCZ 56962 (5); morphometrics—LACM 33603–18 (2), LACM 33696–11 (2), MCZ 28500 (2), MCZ 35185 (1), MCZ 35187 (1), MCZ 56962 (5).

Group E. South African region: meristics (22) and morphometrics (26); for details see Table 3.

Morphometric data (expressed as the range of the measurement as a percentage of SL) for these groups are given in Table 2. Scatter plots of relevant morphometrics are given in Figures 1–3, and meristic data are presented in Figure 4.

TABLE 3

Triphoturus nigrescens. Collection data on SAM specimens.

SAM Cat. no.	Station no.	Date	Position	Depth (m)	Gear	No.	Size (mm)	Remarks
27309	IK 6	23.04.1961	west of Cape Town	200–0	IKMT	1*	—	meristics only
27310	A 2967	28.03.1964	37°45'S 18°00'E	600–0	IKMT	1	32,7	
27311	A 1896	11.07.1962	34°12'S 28°24'E	1000–0	N200B	1	33,4	
27312	A 2961	22.03.1964	40°12'S 14°41'E	700–0	IKMT	1	25,4	
28091	SM 125	10.05.1977	30°32,2'S 30°57,5'E	415–0	RMT	1	28,2	
28092	SM 153	17.05.1977	30°15,5'S 31°28,2'E	664–0	RMT	1	31,8	
28093	SM 148	17.05.1977	30°17,1'S 31°25,2'E	750–0	RMT	3*	—	meristics only
28094	SM 157	18.05.1977	30°05,5'S 31°57,0'E	750–0	RMT	1	33,0	
28308	SM 190	01.06.1978	34°06,3'S 27°08,3'E	658–0	RMT	3	23,3–27,9	
28324	SM 173	28.05.1978	33°25,2'S 27°54,7'E	683–0	RMT	1	30,8	
28346	SM 167	27.05.1978	33°10,5'S 28°17,5'E	1091–0	RMT	1	24,95	
29040	SM 104D	24.05.1976	28°25,6'S 32°44,5'E	200–0	Bongo	1	17,0	
29062	SM 70D	20.05.1976	27°23,9'S 33°02,9'E	200–0	Bongo	1	16,2	
29070	SM 143D	15.05.1977	31°14,7'S 30°14,7'E	212–0	Bongo	2	17,9–28,6	
29146	SM 80	21.05.1976	27°39,0'S 33°00,0'E	359–0	Bongo	1	13,1	
29365	SM 62S	19.05.1976	27°10,2'S 33°10,3'E	45–0	Bongo	1	26,1	
29791	2013	09.08.1982	33°40,0'S 14°41,8'E	50	RMT-2	2	20,3–29,2	
29956	2023	10.08.1982	33°36,08'S 15°45,25'E	75	RMT-2	1	21,6	
29979	2028	11.08.1982	33°40'S 16°45'E	75	RMT-2	1	26,9	
30016	2070	16.08.1982	29°27'S 14°14'E	25	RMT-2	1	19,8	

*—damaged

DISCUSSION

As pointed out by Johnson & Feltes (1984), the interpretation of serial meristic data is difficult, since variation can be the result of ecophenotypic effects (Barlow 1961; Fowler 1970; Johnson & Barnett 1975). Myctophid taxonomy, however, is based on the nature and orientation of various established photophore groupings. These are, in the main, species-specific, although there may be some minor variation in individual photophore position, e.g. the position of SAO_1 in relation to VO_2 – VO_3 in *Lampanyctus ater*. In a few cases (*Protomyctophum normani*-complex and *Symbolophorus boops*-complex) photophore grouping and position may be identical, so that the structure of the secondary sexual characters (the supra- and infracaudal glands) has been employed in distinguishing the species, particularly in the subfamily Myctophinae (Hulley 1981). However, in the tribe Lampanyctini (subfamily Lampanyctinae), the lengths of the supra- and infracaudal glands, rather than differences in structural form, are of diagnostic value, e.g. *Ceratoscopelus* spp., *Lampadena* spp., *Lampanyctus* spp., *Taaningichthys* spp. Variations in the total number of gill rakers on the first arch and variation in the counts of serial meristic characters (fin rays, AO photophores) are of lesser importance, although some exceptions do occur, e.g. in the genera *Notoscopelus* and *Gymnoscopelus*. The number of gill rakers on the lower limb of the first arch may exhibit clinal variation, e.g. *Hygophum taaningi*, while variation in the number on the upper limb of the first arch may be indicative of population structure (*Diaphus dumerilii*, *Hygophum hygommii*, *Lampanyctus alatus*) or may be species-specific, when supported by differences in photophore grouping and/or caudal gland structure (Hulley 1981).

In the *Triphoturus nigrescens* species-group, comprising specimens from the South African region (Group E) and the types of *Lampanyctus microchir*, *Myctophum micropterygum* and *M. nigrescens* (Figs 6–7), the VLO is on or before the vertical through the ventral base; PVO_1 is positioned slightly in front of, on, or behind the vertical through PVO_2 ; and only the VO_2 is elevated and anteriorly displaced to before VO_1 . While VO_3 may be slightly raised in some specimens, it is well below the line passing through VO_2 and SAO_1 . Further, PO_3 is level with PO_2 and PO_5 and Pol_2 is well in front of the adipose origin. Some variation in individual photophore position does occur, namely PO_4 ; PVO_1 ; PVO_2 ; PLO ; SAO_1 (see Description), but this variation is of no taxonomic significance, being encountered even amongst specimens from the same haul. In all specimens of this species-group, the length of the infracaudal gland is less than one-half the length of the caudal peduncle.

In the *T. mexicanus* species-group, comprising specimens from Groups A, B, C, and D, and including the types of *Myctophum mexicanum* and *M. oculateum* (Fig. 5), the VLO is well behind the vertical through the pelvic base; PVO_1 is well before the vertical through PVO_2 ; and both VO_2 and VO_3 are highly elevated, with VO_3 touching the line passing through VO_2 and SAO_1 —the VO_2 is more anteriorly displaced (on vertical through outer ventral base) in the *T. mexicanus* species-group than it is in the *T. nigrescens* species-group (behind vertical

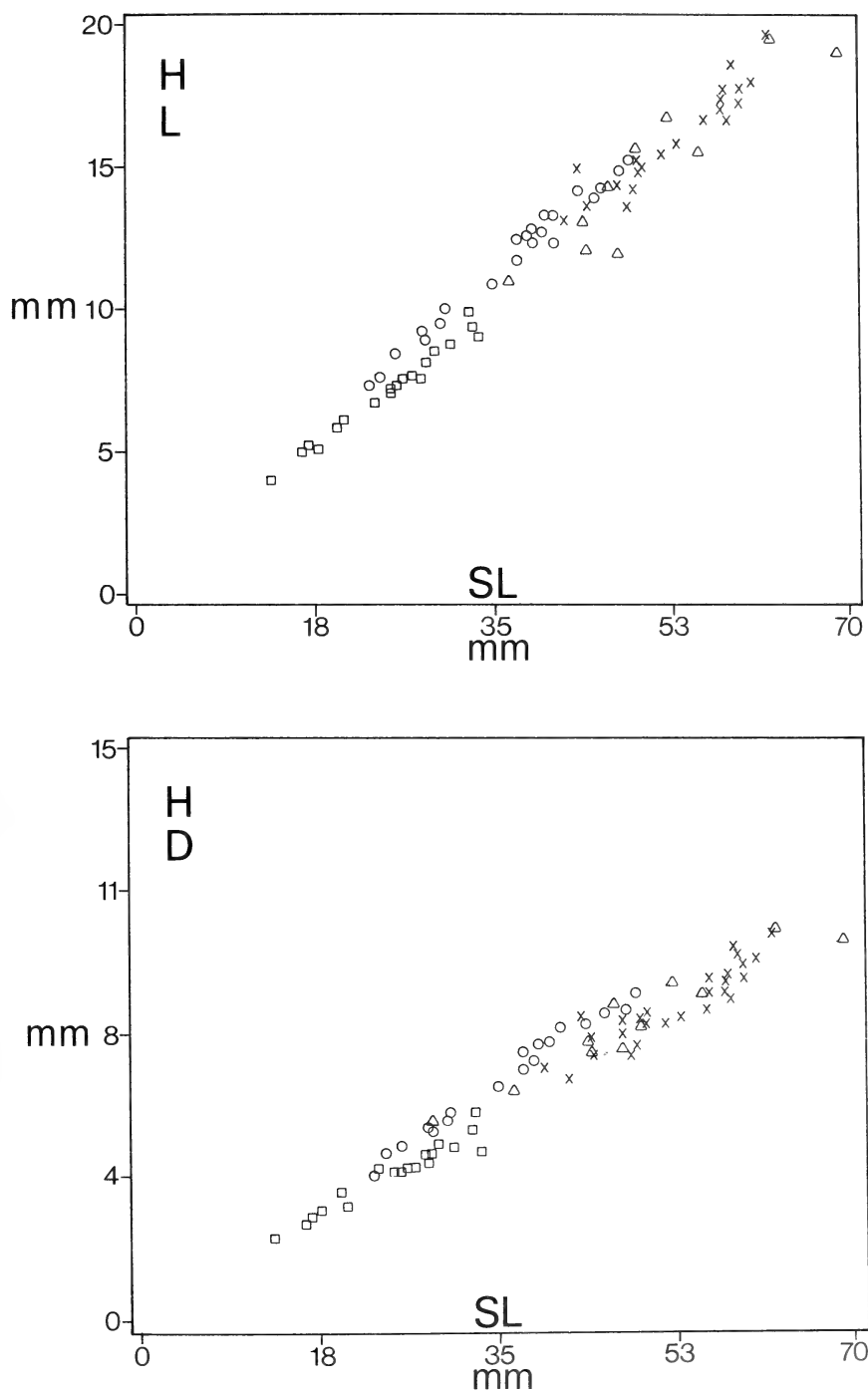


Fig. 1. *Triphoturus*. Upper: head length (HL) plotted against standard length (SL). Lower: head depth (HD) plotted against standard length (SL). Symbols: specimens from Group A, California Current region—cross; Group B, Gulf of California region—circle; Group D, Central and eastern South Pacific region—triangle; Group E, South African region—square. All measurements in mm.

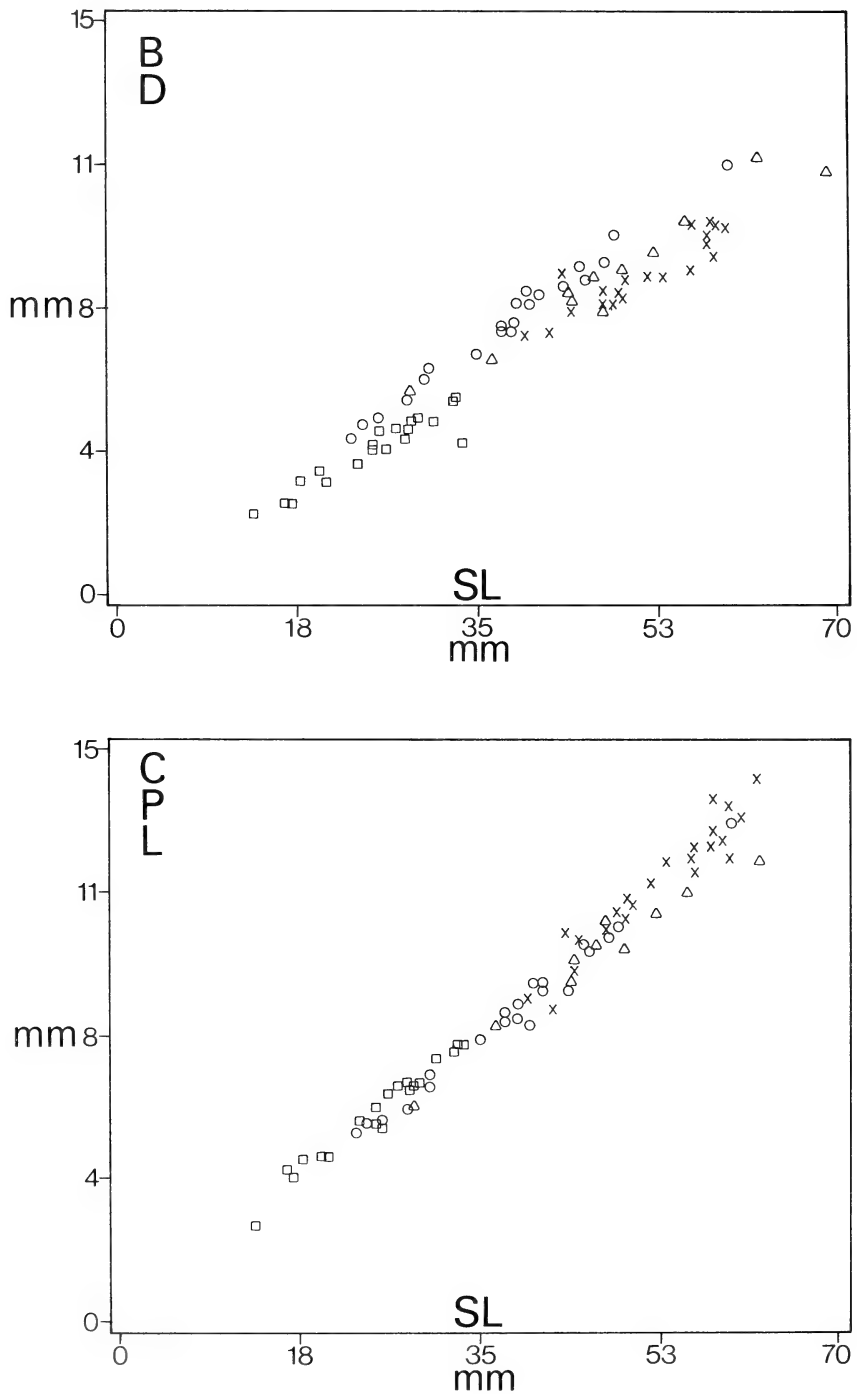


Fig. 2. *Triphoturus*. Upper: body depth (BD) plotted against standard length (SL). Lower: caudal peduncle length (CPL) plotted against standard length (SL). Symbols as in Figure 1. All measurements in mm.

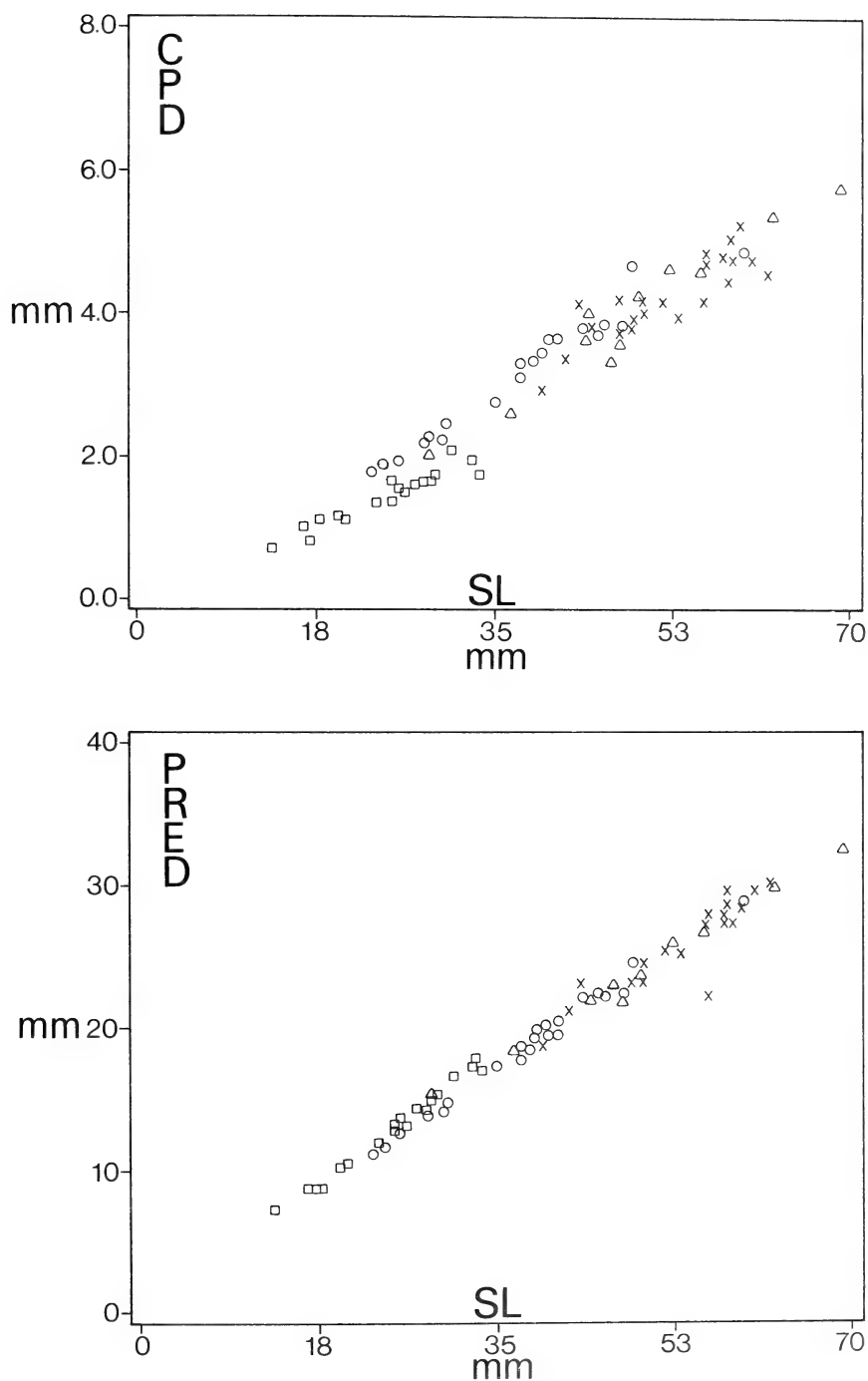


Fig. 3. *Triphoturus*. Upper: caudal peduncle depth (CPD) plotted against standard length (SL). Lower: predorsal length (PRED) plotted against standard length (SL). Symbols as in Figure 1. All measurements in mm.

through outer ventral base) (Figs 5, 7). The PO_3 is raised out of the series and Pol_2 is typically on or behind the vertical through the adipose origin. Atypically (one specimen only), Pol_2 may be situated slightly in advance of the vertical through the adipose origin (Fig. 5A). Variation in individual photophore position also includes the PO_4 , PVO_1 , SAO_1 , SAO_2 , and Prc_2 photophores (see Description). Such intraspecific variation is well documented in the closely related genus *Lampanyctus* (Nafpaktitis *et al.* 1977; Hulley 1981) and has no specific taxonomic value. Infracaudal gland structure in specimens of the *T. mexicanus* species-group is similar and the infracaudal gland always extends more than 70 per cent of CPL. It is therefore concluded that photophore pattern and infracaudal gland structure and length would substantiate the identification of only two species.

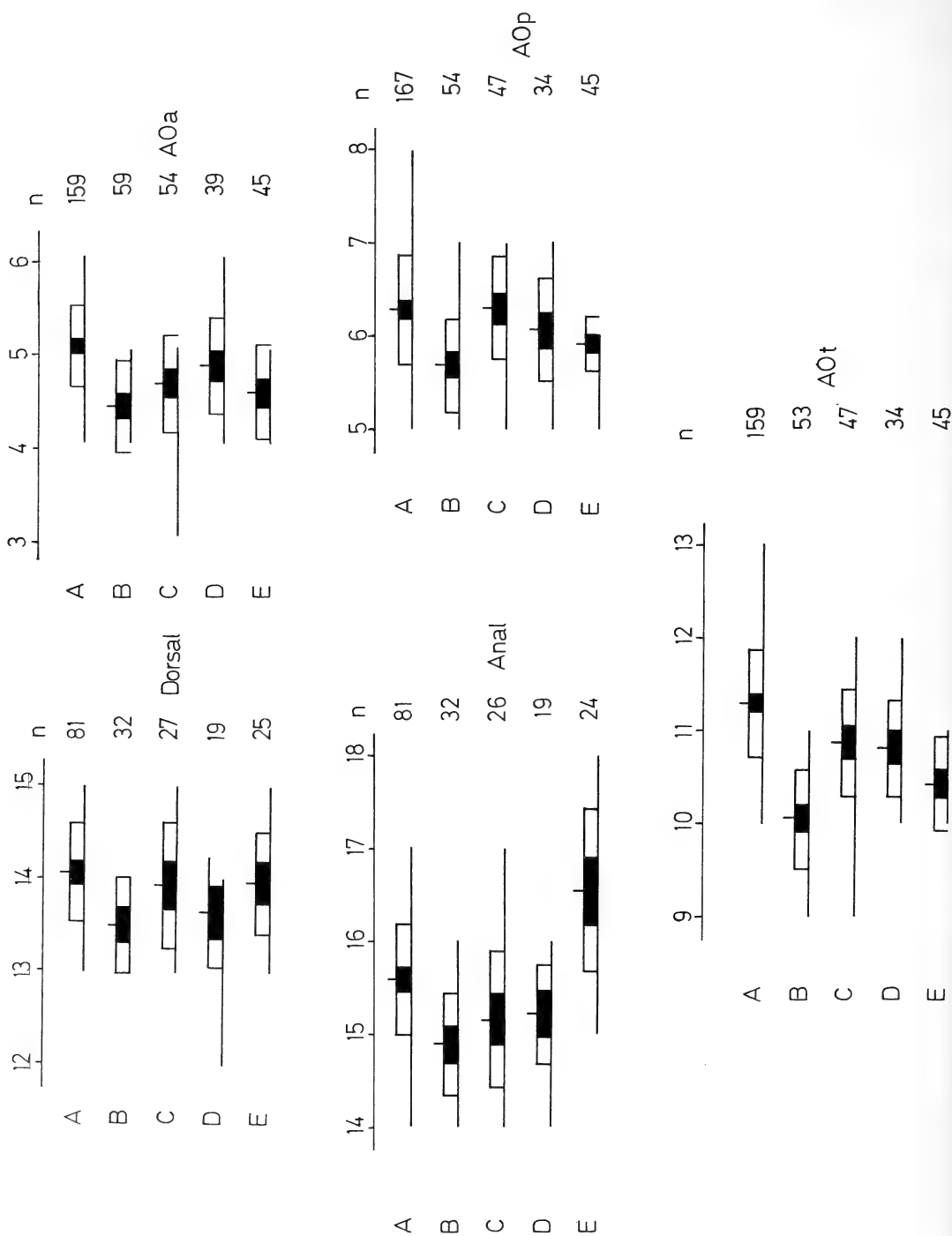
Anal and GRI values (and consequently GRt) would support this conclusion (Fig. 4), as would differences in maximum size. Specimens in the *T. nigrescens* species-group attain a maximum SL of about 40 mm (Nafpaktitis & Nafpaktitis 1969; Wisner 1976; Parin *et al.* 1977; Hulley 1984, in press); the value of 74 mm for *M. micropteryum* given by Weber & de Beaufort (1913) is erroneous, since it is based on the length given by Brauer (1906) for ZMB 17614, now known to be *Lampanyctus isaaci* (Hulley 1981). Specimens in the *T. mexicanus* species-group attain a maximum SL of about 70 mm in both the eastern North and eastern Central-South Pacific (Bolin 1939; Beebe & Van der Pyl 1944; Bussing 1965; Berry & Perkins 1966; Craddock & Mead 1970; Parin *et al.* 1973; Wisner 1976; Childress *et al.* 1980; Neighbours & Nafpaktitis 1982; Imsand 1982). Holton (1969) reported a maximum (?total) length of 100 mm for specimens from off California. The employment of maximum size as a diagnostic should, however, be treated with extreme caution, since it is known that certain myctophids (e.g. *Diaphus brachycephalus*) exhibit dwarfing, i.e. smaller maximum size and smaller size at sexual maturity, in regions of low primary productivity within their distributional range (Hulley 1981).

The *T. mexicanus* species-group is said to comprise two species and a possible subspecies, based on vertebral and gill-raker counts. However, the general tendency is for teleost populations living in warm waters to have less vertebrae than closely related populations living in cool waters, and that these differences are due, in the main, to environmental temperatures prevailing during early development (Fowler 1970; Johnson & Feltes 1984). Modal values and ranges in vertebral counts for specimens from the Gulf of California (32; 30–33) are less than those for specimens from the California Current region (34; 32–36) (Wisner 1976, table 27) and may well be associated with differences in surface water temperatures in the two areas during the spring–summer spawning peak (Ahlstrom 1972; Imsand 1974, 1982; Moser *et al.* 1974). Concomitant with these differences in vertebral count, are differences in serial meristics. Specimens from the Gulf (Group B) have a significantly lower number of dorsal ($t = -5.12$ df 111) and anal ($t = -5.80$ df 111) fin rays, and AOa ($t = -9.45$ df 216) and AOp ($t = -6.63$ df 214) photophores than specimens from the California Current region

(Group A) (Fig. 4). Group B specimens also vary from Group A specimens in possessing higher GRI, and hence GRt counts (t 6,95 df 111; t 6,63 df 111, respectively). The low weighting to the taxonomic significance of GRI variation has already been noted above. Therefore the recognition of a separate subspecies for the Gulf of California specimens does not appear to be warranted. This is supported by the fact that values for D, A, AOa and AOp counts of specimens from the Middle American Trench (Group C), just to the south of the mouth of the Gulf, appear to be somewhat intermediate between those of Groups A and B (Fig. 4). Both GRu and GRI counts in these Group C specimens approximate those for California Current region (Group A) specimens.

Specimens from the eastern Central and South Pacific (Group D: representing *T. oculeus*) may be distinguished meristically from specimens from Middle American Trench (Group C) only by their lower number of gill rakers (GRu: t -14,29 df 46; GRI: t -8,37 df 46; GRt: t -11,56 df 46). Dorsal, anal and AO counts are not significantly different, and mirror equivalent modal values and ranges in vertebral count (Wisner 1976, table 27). The identity of *T. oculeus* is therefore based solely on gill-raker count and on pigmentation of the larvae (Moser & Ahlstrom 1970; Ahlstrom 1971). However, the taxonomic value of these gill-raker differences at the species level is questionable, especially in view of the lack of diagnostic photophore characters. As pointed out above, variations in gill-raker count (both GRu and GRI values) may not be species-specific, especially when they are not corroborated by differences in photophore grouping and/or supra- and infracaudal gland structure. Gill-raker variation is then only interpreted in terms of population differences. This is applicable to both geographically continuous populations (*Diaphus dumerilii*) and to geographically separated populations (*Hygophum hygomii*) (Hulley 1981), as is probably the case in Group D specimens. This is supported by the fact that specimens from off Panama and Costa Rica were found to have GR counts both of $3 + 1 + 10$ (9-11) (LACM 33603-18 (3), LACM 33676-7 (4), LACM 33696-11 (4), SU 65711 (2)) and of $4 + 1 + 10-11$ (SU 46829 (2)). Furthermore, one of the syntypes of *Myctophum oculeum* (MCZ 35187) has GR $4 + 1 + 10$ (left side) and GR $3 + 1 + 10$ (right side).

On the other hand, larval characters (including pigmentation) apparently show a considerable degree of variation within a myctophid species: two larval forms of *Hygophum proximum* are found in the northern Indian Ocean (Pertseva-Ostroumova 1974), while only one adult species, exhibiting clinal variation, has been recognized (Nafpaktitis & Nafpaktitis 1969); three larval forms for the *Hygophum macrochir*-complex in the eastern Central Atlantic have been found (Moser & Ahlstrom 1974), but only two adult species are recognized (Nafpaktitis *et al.* 1977; Hulley 1981). Two hypotheses about larval form are therefore possible: either, that one species may have two or more larval forms; or that adults of the second species have not been captured or recognized. In view of the extensive sampling programmes and taxonomic investigations, particularly in the eastern Central Atlantic and the Arabian Sea, the latter hypothesis seems to



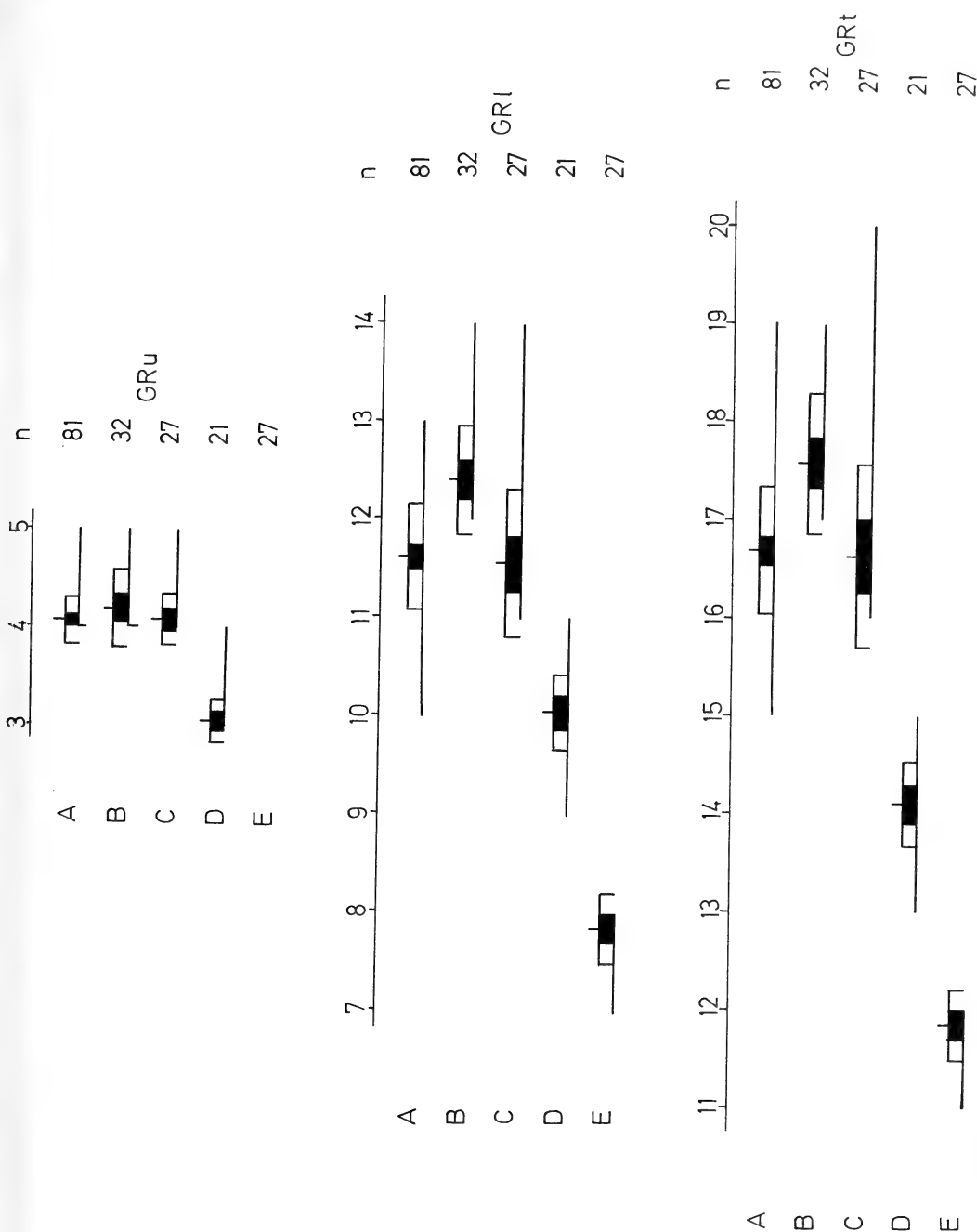


Fig. 4. *Triphoturus*. Meristics plotted according to the method of Hubbs & Hubbs (1953). A—Group A; B—Group B; C—Group C; D—Group D; E—Group E; n = number of counts used to construct the particular graph.

be unlikely for *Hygophum macrochir* and *H. proximum*. Larval diagnostics for *Triphoturus* in the eastern Central Pacific would appear to be unresolved as yet. Ahlstrom (1971: 31) stated that 'at least two species (my italics) of *Triphoturus* were taken in the EASTROPAC area' (13°N–20°S, 85°W–126°W), a region potentially occupied at least by *T. nigrescens*, *T. mexicanus* and *T. oculus*, if the latter species is valid (*fide* Parin *et al.* 1973, fig. 18; Wisner 1976, fig. 156; and above data for SU 46829). On the evidence presented by meristics and larval characters, Group D specimens are therefore not considered specifically distinct, and at best can only be recognized as a 'southern' population of *T. mexicanus*.

Morphometric values (Table 2) would not substantiate the differentiation of more than two species. There is little difference in the scatterplots for the various groups (Figs 1–3), although in general, specimens of Group E (corresponding to *T. nigrescens*) appear to be more slender, with the origin of the dorsal fin located somewhat more posteriorly than in Groups A, B, C, and D (corresponding to *T. mexicanus*) (Figs 2–3). Analysis of the data reveals that there is a significant ($F = 6.86$ df 1, 87) difference in the case of the slopes of the regressions of CPD vs SL when Group E data are compared to combined data for Groups A, B, C, and D.

In summary then, the genus *Triphoturus* is considered to comprise only two species, *T. nigrescens* and *T. mexicanus*, the latter with a 'northern' and a 'southern' population. Specimens from the Gulf of California represent ecophenotypic variants of the 'northern' population.

SYSTEMATIC ACCOUNT

Genus *Triphoturus* Fraser-Brunner, 1949

Type-species. *Myctophum (Lampanyctus) micropterus* Brauer, 1906 (= *Myctophum (Lampanyctus) nigrescens* Brauer, 1904) (by original designation).

Mouth large, jaws extending well behind vertical through posterior margin of orbit, with maxillary abruptly enlarged posteriorly. Base of anal fin longer than base of dorsal fin. Pectoral fins small. Dn absent, Vn present. Five PO, with PO₄ elevated and anteriorly displaced to above PO₃. VLO at or a little above lateral line. Five VO, with VO₂ elevated and anteriorly displaced to in front of the vertical through VO₁, and with VO₃ either level, raised or elevated. SAO series markedly angulate. AO series divided into AOa and AOp, both level. Two Pol. Three Prc in an oblique line. Series of overlapping, luminous scales supracaudally and infracaudally in both sexes, immediately in front of procurent caudal rays.

Two species.

KEY TO SPECIES

- 1a. VO₃ highly elevated, touching line through VO₂ and SAO₁; PO₃ raised out of series; VLO well behind vertical through outer ventral base; GR 3–5 + 1 + 9–14, total 13–20 *T. mexicanus*

- 1b. VO_3 level or raised, but always well below line joining VO_2 and SAO_1 ; PO_3 level with PO_2 and PO_5 ; VLO on or before vertical through outer ventral base; GR 3 + 1 + 7–8, total 11–12 *T. nigrescens*

Triphoturus mexicanus (Gilbert, 1890)

Fig. 5

- Myctophum mexicanum* Gilbert, 1890: 51 (lectotype USNM 76343—Gulf of California; paralectotypes SU 68 (3)—25°59'45"N 111°03'30"W; Böhlke 1953).
Scopelus mexicanus Lütken, 1892: 266.
Nannobranchium mexicanum Goode & Bean, 1895: 512.
Myctophum ocaleum Garman, 1899: 260, pl. LVI, fig. 2 (19 syntypes: MCZ 28500, 34945, 34946, 35162, 35182, 35185, 35187, 35189, USNM 120422—eastern Pacific; Paxton 1979).
Myctophum (Lampanyctus) mexicanum Brauer, 1904: 396.
Myctophum (Lampanyctus) ocaleum Brauer, 1906: 167.
Lampanyctus mexicanus: Parr, 1928: 84 (key); 1931: 25 (key), 30, fig. 12. Bolin, 1939: 135, fig. 21. Beebe & van der Pyl, 1944: 84, fig. 17.
Lampanyctus ocaleus: Parr, 1928: 85 (key).
Lampanyctus (Triphoturus) mexicanus: Fraser-Brunner, 1949: 1084, fig. (key). Berry & Perkins, 1966: 660, fig. 22C.
Triphoturus mexicanus: Bussing, 1965: 203. Bekker, 1967: 179. Paxton, 1967: 424, figs 11, 14, 16. Ahlstrom, 1969: 41; 1971: 31; 1972: x, 64–124. Craddock & Mead, 1970: 3.31. Ebeling *et al.*, 1970: 4, figs 1–4. Robison, 1972: 448, figs 3–4. Paxton, 1972: 6. Brewer, 1973: 23, fig. 10B. McNulty & Nafpaktitis, 1976: 579, pls 1–8. Childress *et al.*, 1980: 28, figs 1, 4. Pieper & Bargo, 1980: 935, figs 1–4. Neighbors & Nafpaktitis, 1982: 208, figs 1, 2. Barnett, 1983: 248. Loeb *et al.*, 1983a: 134; 1983b: 155, figs 1, 2, 7.
Triphoturus ocaleus: Ahlstrom, 1971: 31.

Material

Types. *Myctophum mexicanum*: lectotype, USNM 76343; paralectotypes, SU 68 (2). *Myctophum ocaleum*: syntypes, MCZ 28500 (3), 35185 (1), 35187 (1).
Other. CAS 24312 (30), Santa Catalina Islands; CAS 47824 (5), off Baja California; LACM 31125–27 (27), Middle American Trench (22°21'N 108°12'W–22°25'N 108°29'W); LACM 33603–18 (3), 08°57'30"N 88°05'00"W; LACM 33696–11 (4), 05°28'00"N 82°10'00"W; LACM 33676–7 (4), 05°29'30"N 82°33'00"W; LACM 39201–1 (48), San Pedro Basin (010°T from Long Point Light, 6.0 miles); SAM–24926 (3), 33°40'N–33°45'N, 118°27'W–118°18'W; SAM–30897 (5), 33°19'S 73°39'W; SU 46808 (30), Gulf of Mexico; SU 46829 (2), Panama; SU 65711 (2), Panama.

Description

Meristics and measurements are given in Tables 1–2 and Figure 4.

Origin of dorsal fin well behind vertical through ventral base, usually nearer to tip of snout than to end of lateral line; origin of anal fin under middle of dorsal base or slightly more posterior; origin of adipose fin about on vertical through last anal ray. Pectoral fins small, reaching to about PO_4 ; ventral fins extending slightly posterior to VO_4 .

Dn absent; Vn small, at anteroventral margin of orbit. Op_2 at about level of upper, expanded end of maxillary. Five PO , with PO_1 – PO_2 interspace greatest,

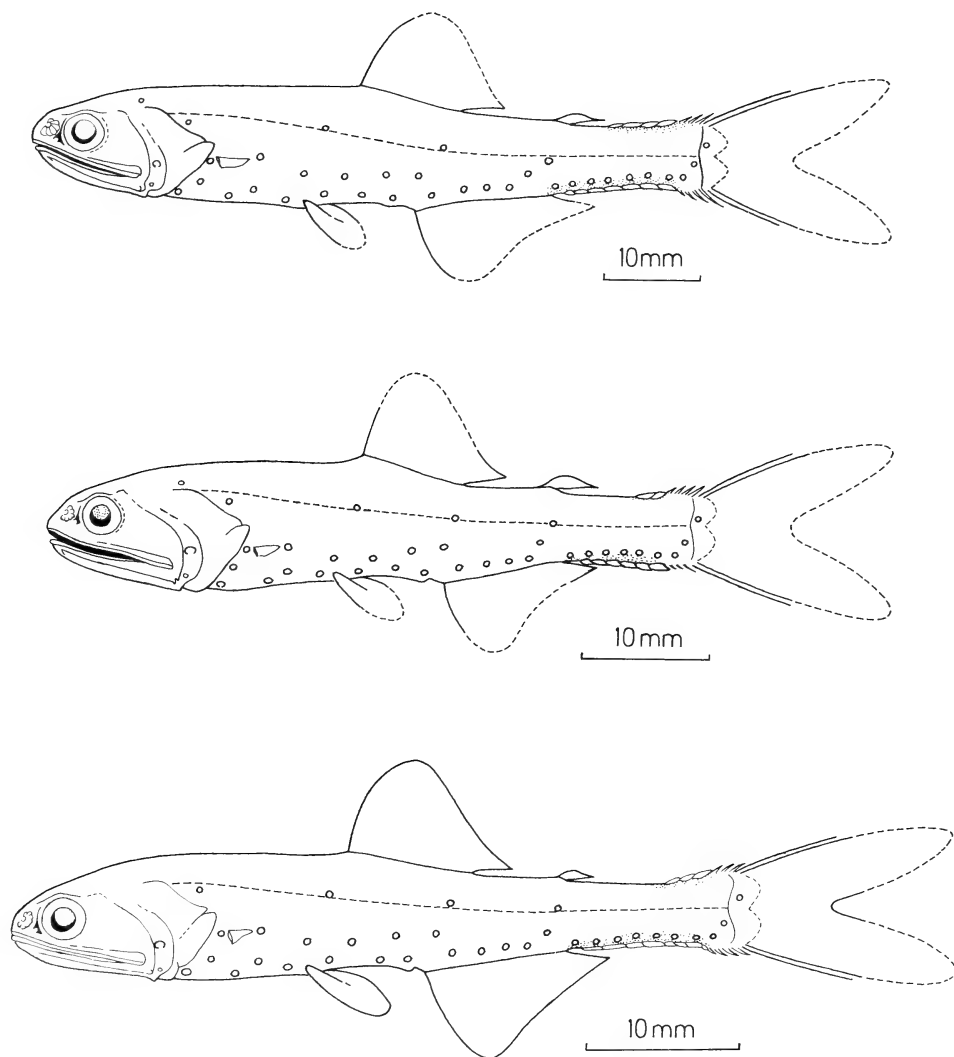


Fig. 5. *Tripoturus mexicanus*. Upper: southern population (MCZ 56962, 33°19'S 73°39'W, SL 68,7 mm). Middle: northern population (SU 46808, Gulf of California, SL 49,5 mm). Lower: northern population (LACM 39201-1, San Pedro Basin, California, SL 47,6 mm).

with PO_3 raised, and with PO_4 elevated and anteriorly displaced to directly on or slightly behind vertical through PO_3 and at level of upper pectoral base or higher. PVO_1 above PO_1 – PO_2 interspace, closer to PO_1 than to PO_2 and below level of Op_2 ; PVO_2 well behind vertical through PVO_1 and below level of upper end of pectoral base. PLO well in advance of vertical through PVO_1 , about one photophore diameter below lateral line. VLO behind vertical through ventral base, on vertical through VO_1 , and touching dorsal edge of lateral line. Five VO , with VO_2 highly elevated and anteriorly displaced to vertical through outer ventral base; with VO_3 highly elevated, touching line joining VO_2 and SAO_1 . SAO series markedly angulate; with SAO_1 midway between VO_4 and VO_5 or closer to VO_5 and slightly above level of VO_2 ; with SAO_2 above or slightly behind anal origin and at or above level of SAO_1 ; and with SAO_3 behind vertical through anal origin, touching dorsal edge of lateral line. AOa level, with AOa^1 – AOa^2 interspace greatest; AOp level, all behind base of last anal ray. Two Pol , with Pol_1 behind last AOa , and with Pol_2 on or behind vertical through adipose origin, touching dorsal edge of lateral line. Three Prc , in straight ascending line, with Prc_2 nearer to Prc_1 and on or touching line through centres of Prc_1 and Prc_3 , and with Prc_3 above level of lateral line.

Supracaudal gland consisting of 3–4 overlapping, luminous scales; infracaudal gland elongate (greater than 70% CPL), with 4–7 overlapping, luminous scales.

Maximum length about 70 mm.

Distribution

Vertical distribution. California Current region: day 200–700 m (maximum 400–500 m), night 50–200 m (maximum 100–200 m). Gulf of California: day 200–700 m (maximum 400–500 m), night 25–550 m (maximum 200–300 m) (Imsand 1982).

The geographic distribution of the species is given in Figure 8.

Triphoturus mexicanus apparently possesses a disjunct distribution in the eastern Pacific Ocean. It is known from throughout the Gulf of California, where it is the dominant midwater fish species between 25°N and 29°N. In the California Current region the species occurs between 38°N and about 20°N, but offshore may extend southwards to 13°N at 127°W. Off the coasts of Central and South America it has been taken from 13°N to about 35°S. Towards its southern limit the species has only been recorded east of 76°W, but off the coast of Peru it may extend westwards to about 95°W.

Triphoturus nigrescens (Brauer, 1904)

Figs 6, 7

Myctophum (Lampanyctus) nigrescens Brauer, 1904: 403 (syntypes: ZMB 17617—03°24'06"S 58°38'01"E; ZMB 22379—02°38'09"S 63°37'09"E); 1906: 241, fig. 158.

Myctophum (Lampanyctus) micropteron Brauer, 1906: 239, fig. 157 (*partim*) (lectotype: ZMB 17616: 02°43'08"S 61°12'06"E; Hulley 1981: 205).

- Lampanyctus microchir* Gilbert, 1913: 101 (holotype: USNM 74468—Suruga Bay, Japan). Parr, 1928: 85 (key).
- ?*Myctophum micropterus*: Weber & de Beaufort, 1913: 154, fig. 59.
- non *Myctophum* (*Lampanyctus*) *micropterus*: Pappenheim, 1914: 197 (= *Lampanyctus isaacsi* Wisner, 1974).
- Lampanyctus nigrescens*: Parr, 1928: 84 (key).
- Lampanyctus micropterus*: Parr, 1928: 85 (key).
- Lampanyctus* (*Triphoturus*) *microchir* Fraser-Brunner, 1949: 1083, fig. (key). Berry & Perkins, 1966: 660, fig. 22C.
- Lampanyctus* (*Triphoturus*) *micropterus* Fraser-Brunner, 1949: 1083, fig. (key).
- Lampanyctus* (*Triphoturus*) *nigrescens* Fraser-Brunner, 1949: 1083, fig. (key). Berry & Perkins, 1966: 660, fig. 22C.
- Triphoturus microchir*: Bekker, 1967: 179. Nafpaktitis & Nafpaktitis, 1969: 55, figs 62, 70. Legand *et al.*, 1972: 306, fig. 27. Kotthaus, 1972: 29, fig. 284. Clarke, 1973: 406, fig. 12; 1980: 625, figs 1–4. Hartmann & Clarke, 1975: 636. Parin *et al.*, 1973: 114, fig. 19; 1977: 125, fig. 21.
- Triphoturus nigrescens*: Paxton, 1972: 6. Wisner, 1976: 165, fig. 155. Loeb, 1979a: 178; 1979b: 789, fig. 10; 1980: 192. Barnett, 1983: 284; 1984: 201. Hulley, 1984: 90, fig. 19. Paxton *et al.*, in press.

Material

Types. *Lampanyctus microchir*: holotype, USNM 74468. *Myctophum* (*Lampanyctus*) *micropterus*: lectotype, ZMB 17616. *Myctophum* (*Lampanyctus*) *nigrescens*: syntypes, ZMB 17617, 22379.

Other. See Table 3.

Description

Meristics and measurements are given in Tables 1–2 and Figure 4.

Origin of dorsal fin well behind vertical through ventral base, nearer to end of lateral line than to tip of snout; origin of anal fin under middle of dorsal base or slightly more anterior; origin of adipose fin on vertical through base of last anal ray. Pectoral fins small, reaching to about PO₄; ventral fins extending slightly posterior to VO₄.

Dn absent; Vn small, at anteroventral margin of orbit. Op₂ at about level of upper, expanded end of maxillary. Five PO, with PO₁–PO₂ interspace greatest and with PO₄ elevated and anteriorly displaced to directly on, anterior to, or behind vertical through PO₃ and at level of upper pectoral base or higher. PVO₁ above PO₁–PO₂ interspace, closer to PO₁ than to PO₂ and at about level of Op₂; PVO₂ on or only slightly behind vertical through PVO₁ and below level of upper pectoral base. PLO well in advance of vertical through upper pectoral base, at or less than one photophore diameter below lateral line. VLO slightly anterior to vertical through ventral base, touching dorsal edge of lateral line. Five VO, with VO₂ highly elevated and anteriorly displaced to before vertical through VO₁; VO₃ level or somewhat raised, never touching line joining VO₂ and SAO₁. SAO series markedly angulate, with SAO₁ above VO₃–VO₄ interspace or above VO₄ and at about level of ventral margin of orbit, with SAO₂ above anal origin and at level of SAO₁, and with SAO₃ behind vertical through anal origin, touching dorsal edge of lateral line. AOa level, with AOa¹–AOa² interspace greatest; AOp level, all behind base of last anal ray. Two Pol, with Pol₁ behind last AOa

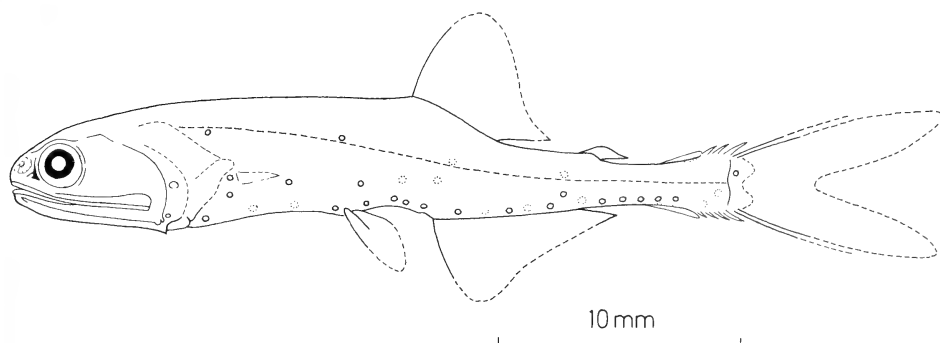


Fig. 6. *Triphoturus nigrescens*. Syntype (ZMB 17617, 'Valdivia' Station 231, 03°24'06"S 58°38'01"E, SL 29,3 mm), now designated as lectotype.

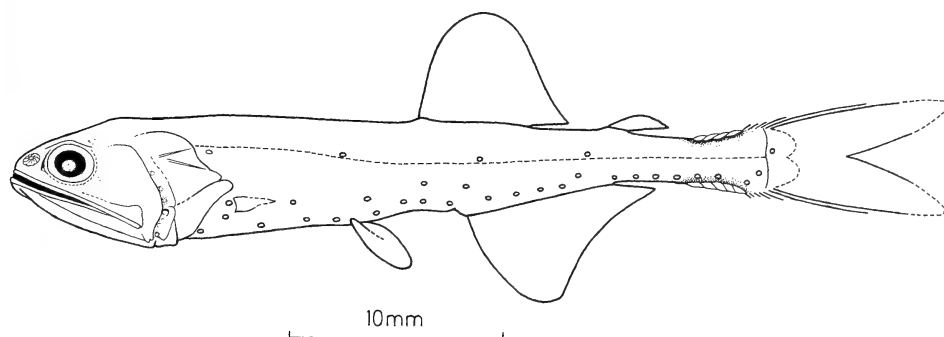


Fig. 7. *Triphoturus nigrescens* (SAM-28094, 30°05,5'S 31°57,0'E, SL 33,6 mm).

and with Pol_2 in advance of vertical through adipose origin, touching dorsal edge of lateral line. Three Prc , in straight ascending line, with Prc_2 nearer Prc_1 and touching line through centres of Prc_1 and Prc_3 , and Prc_3 above level of lateral line.

Supracaudal gland consisting of four overlapping, luminous scales; infracaudal gland short (less than 50% CPL), with five overlapping, luminous scales.

Maximum length 40 mm.

Remarks

Due to the poor state of preservation of one (ZMB 22379) of the two syntypes (Table 1), specimen ZMB 17617 is here designated the lectotype of *Myctophum* (*Lampanyctus*) *nigrescens* Brauer, 1904. Comparison of this lectotype with the holotype of *Lampanyctus microchir* Gilbert (USNM 74468) and the lectotype of *Myctophum* (*Lampanyctus*) *micropterum* Brauer (ZMB 17616) indicates that only a single species is involved. GR counts are similar (3 + 1 + 8,

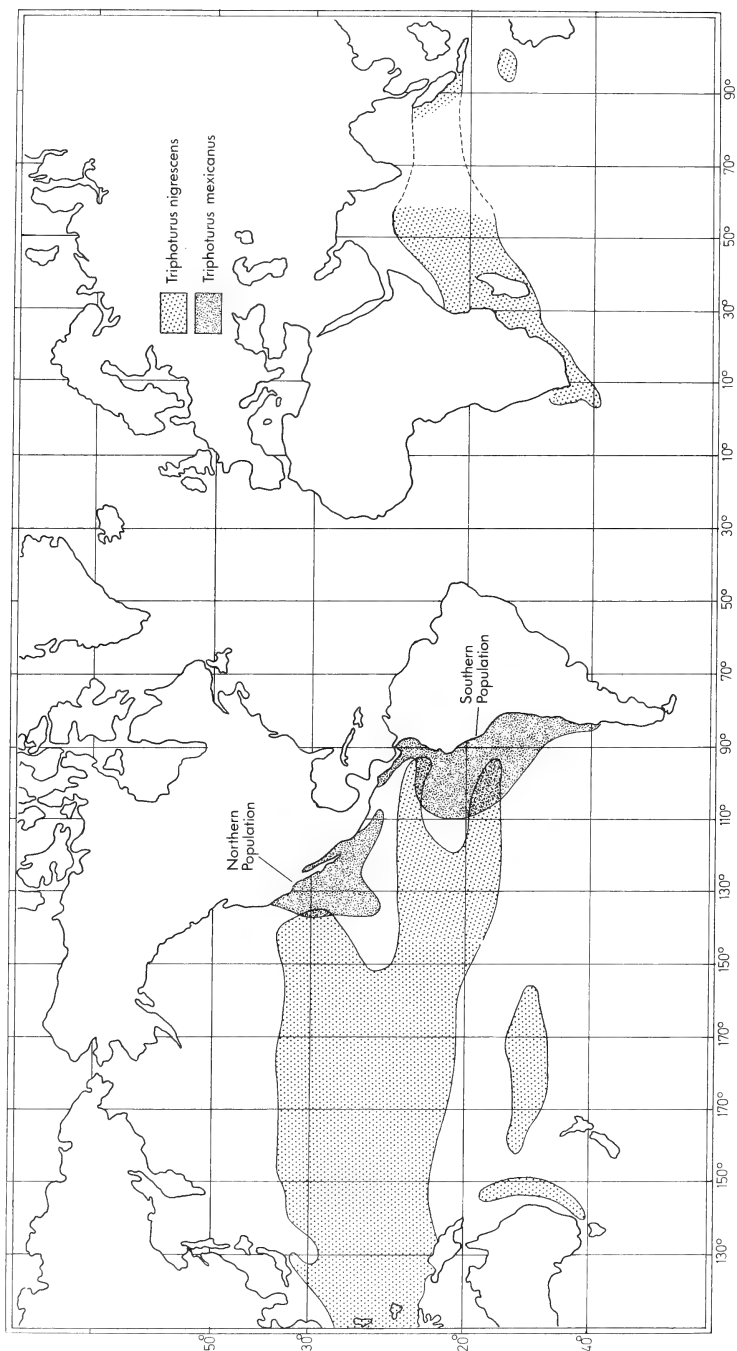


Fig. 8. Distribution of *Triphoturus mexicanus* and *Triphoturus nigrescens*.

total 12), PO_3 is level with PO_2 and PO_5 , and VLO is anterior to the vertical through the outer ventral base in all three specimens. Further, in the three specimens the infracaudal gland is shorter than 40 per cent of CPL. Some minor differences in individual photophore position were observed: VO_3 is level with the rest of the series in *L. microchir* and *M. nigrescens*, but slightly raised in *M. micropterus*; SAO_1 is directly above VO_4 in *M. micropterus*, but slightly in advance of the vertical through that photophore in *L. microchir* and *M. nigrescens*; and Prc_2 is on the line joining Prc_1 and Prc_3 in *M. nigrescens*, touches the line in *L. microchir*, and is slightly below the line in *L. micropterus*. Such variation is mirrored in the South African population. Due to damage, D and A counts were not possible for *L. microchir* but the values given by Gilbert (1913) (14 and 17 respectively) fall within the range for *Triphoturus nigrescens* (Fig. 4).

Distribution

Vertical distribution. Off Hawaii: adults day 400–900 m (maximum 650–700 m and 900–1 000 m); adults night 200–300 m and 600–1 000 m; juveniles (less than 20 mm SL) showing little diel migration above 400 m (Imsand 1982).

The geographic distribution of the species is given in Figure 8.

Triphoturus nigrescens is an oceanic, mesopelagic, warm-water species. In the Pacific Ocean it is distributed between about 35°N and 38°S, and extends eastwards in a tongue (0°–08°N) to the coasts of Ecuador, Colombia and Panama. It is absent from upwelled waters of the California and Peru currents. In the western North Pacific it reaches at least to 35°N in the Kuroshio Current. The species is known from South-east Asian Seas and from between 22°S and 38°30'S off the east coast of Australia and in the Tasman Sea (Paxton *et al.* in press). It is distributed in the Indian Ocean between 08°N and 15°S and off the west Australian coast (22°S), and has been reported as far south as 34° in the Agulhas Current. Recent data from the Sea Fisheries Research Institute's phyllosoma sampling cruises off the west coast of South Africa has revealed the presence of the species in the pockets of warm Agulhas Water, that round the Cape of Good Hope and occur in the eastern South Atlantic. These specimens represent the first records of the genus and the species in the Atlantic Ocean and are representative of a Broadly Tropical Pattern (Agulhas Subpattern) of distribution (Hulley 1981).

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- ZAR, J. H. 1974. *Biostatistical analysis*. Englewood Cliffs: Prentice-Hall.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers.

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. **SPECIAL HOUSE RULES**

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text

e.g. '... the Figure depicting *C. namacolus* ...': '... in *C. namacolus* (Fig. 10) ...'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names

e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives

e.g. Therocephalia, but therocephalian

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Reference to the author should preferably be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

P. ALEXANDER HULLEY

A TAXONOMIC REVIEW OF THE
LANTERNFISH GENUS *TRIPHOTURUS*
FRASER-BRUNNER, 1949
(MYCTOPHIDAE, OSTEICHTHYES)

ISSN 0303-2515

ANNALS

OF THE SOUTH AFRICAN
MUSEUM



CAPE TOWN

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Title: informative but concise, without abbreviations and not including the names of new genera or species
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FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* 74 (33): 627–634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) 2 (17): 309–320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* 17 (4): 1–51.

THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* 4 (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* 16: 269–270.

(continued inside back cover)

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ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

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THE SOUTH AFRICAN MUSEUM'S
MEIRING NAUDE CRUISES
PART 16
BRACHIOPODA FROM THE
1975–1979 CRUISES

By
NORTON HILLER

Cape Town

Kaapstad

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THE SOUTH AFRICAN MUSEUM'S MEIRING NAUDE CRUISES

PART 16

BRACHIOPODA FROM THE 1975-1979 CRUISES

By

NORTON HILLER

Department of Geology, Rhodes University, Grahamstown, South Africa

(With 19 figures and 1 table)

[MS accepted 3 December 1985]

ABSTRACT

Sixteen species of articulate brachiopods and a single inarticulate brachiopod are recorded from off the east coast of South Africa. Of the seventeen species, *Grammetaria africana*, *Notozyga gracilis* and *Megerlia acurra* are new, and five others are recorded for the first time from South African waters.

CONTENTS

	PAGE
Introduction	97
Previous research	97
List of species	99
Brachiopod distribution	100
Geographic distribution	100
Bathymetric distribution	101
Systematic account	102
Acknowledgements	138
References	139

INTRODUCTION

The present paper deals with a number of brachiopod species that were collected during the *Meiring Naude* cruises in the years from 1975 to 1979 inclusive. The positions of the various sampling stations from which brachiopods were recovered are shown in Figure 1; further data on these stations may be obtained from Louw (1977, 1980). A few specimens that have been separated from coral material of various origins have also been included. Station data for these specimens have been given separately along with the descriptions of the species concerned.

PREVIOUS RESEARCH

Very little research work has been done on the South African brachiopod fauna; the earliest records date from the late eighteenth and early nineteenth centuries and deal with the commonly occurring members of the Kraussinidae. From 1850 onwards a handful of species belonging to other families have been added to the list and described in a number of publications, including the reports

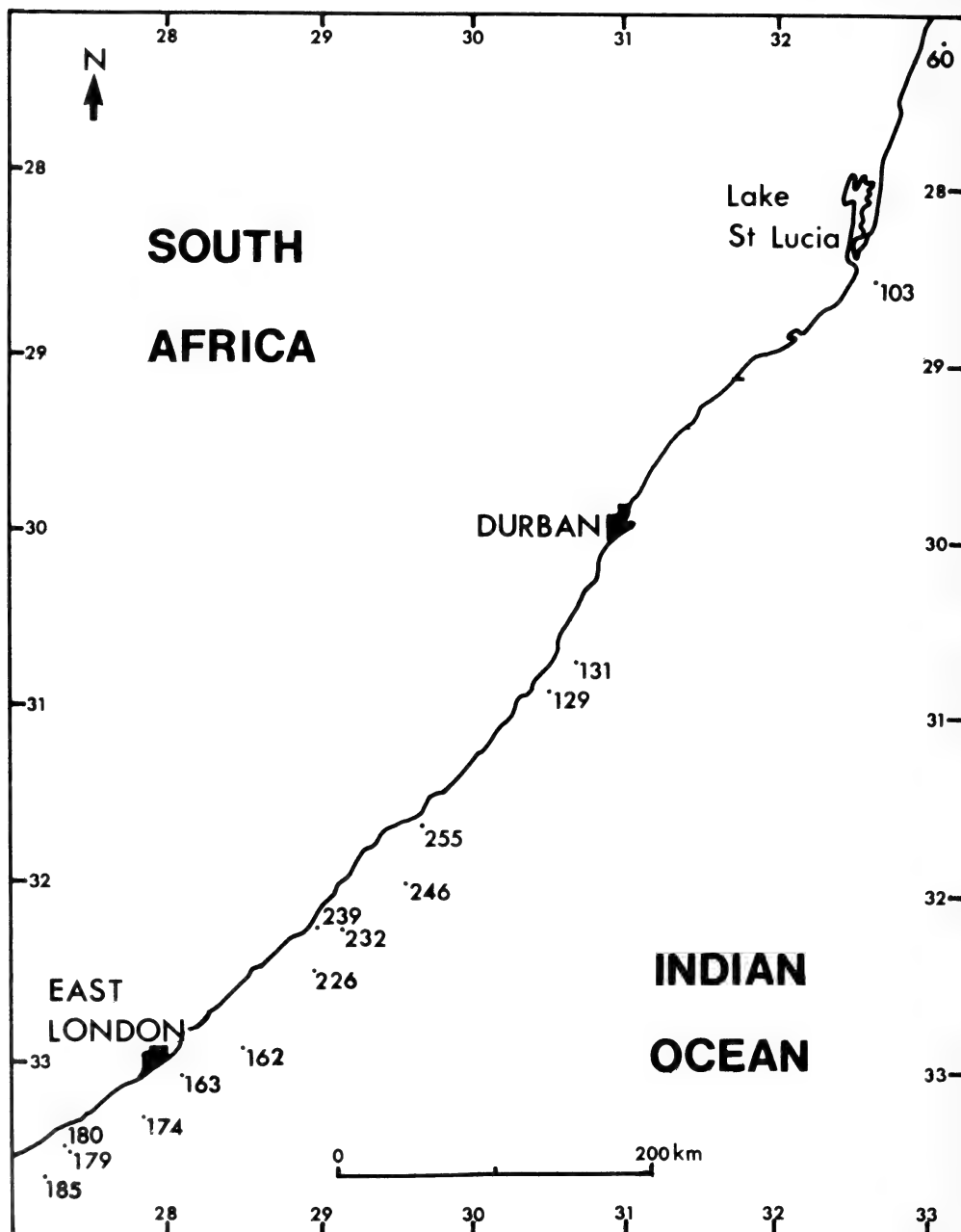


Fig. 1. Map showing locations of SM stations from which brachiopods were recovered during the *Meiring Naude* cruises 1975–1979.

of two major expeditions—the 'Challenger' Expedition (Davidson 1880) and the 'Valdivia' Expedition (Blochmann 1906).

The most comprehensive paper, and the only one dealing specifically with South African brachiopods, was that of Jackson (1952), which includes an account of all the earlier work. Jackson recorded fifteen species belonging to nine genera from a number of stations extending from Saldanha Bay on the west coast round to Delagoa Bay (now Maputo Bay, Mozambique) on the east. Of the forms recorded by Jackson, five—*Crania*, *Agulhasia*, *Terebratulina*, *Kraussina* and *Megerlina*—are recorded again in this paper; two of the species he described from western Cape waters have not, as yet, been found east of Cape Agulhas, viz. *Megathiris capensis* and *Kraussina crassicostata*.

Since the publication of Jackson's work only three papers by Cooper (1973*b*, 1973*c*, 1981) have added to our knowledge of the brachiopods from South African waters. The papers have mostly confirmed previous records but to the list of species they have added *Platidia anomioides* and *Xenobrochus africanus*. Species such as *Chlidonophora chuni* and *Eucalathis fasciculata*, described by Cooper from off Madagascar, can now be added to the South African list.

LIST OF SPECIES

	Station No.	Complete specimens**	Pedicle valves	Brachial valves
Family Craniidae				
<i>Crania</i> sp.	SM 239	1 (1)	—	—
Family Frieleidae				
* <i>Grammetaria africana</i> sp. nov.	SM 232	1 (1)	—	—
Family Dyscoliidae				
* <i>Dyscolia</i> cf. <i>johannisdavisi</i> (Alcock)	SM 174	4 (1)	2	1
<i>Xenobrochus africanus</i> (Cooper)	SM 103	13 (13)	1	—
	SM 129	1 (1)	—	—
	SM 131	—	3	1
	SM 162	—	1	—
<i>Xenobrochus agulhasensis</i> (Helmcke)	SM 232	1	—	—
<i>Xenobrochus</i> ? sp. 1	SM 131	1	—	—
<i>Xenobrochus</i> ? sp. 2	SM 226	—	1	1
	SM 232	—	6	3
Family Cancellothyrididae				
<i>Terebratulina</i> sp.	SM 131	8	1	3
	SM 180	1	—	—
Family Chlidonophoridae				
* <i>Chlidonophora chuni</i> Blochmann	SM 103	2	—	—
	SM 246	3 (2)	—	—
* <i>Notozyga gracilis</i> sp. nov.	SM 131	1	—	—
* <i>Notozyga</i> sp.	SM 131	1	—	—
* <i>Eucalathis fasciculata</i> Cooper	SM 60	4 (4)	—	—
	SM 103	1	—	—
	SM 246	7 (7)	2	2
<i>Agulhasia davidsoni</i> King	SM 131	9	—	—

* New records for South African waters

** Number of live specimens shown in brackets

	Station No.	Complete specimens**	Pedicle valves	Brachial valves
Family Kraussinidae				
<i>Kraussina rubra</i> (Pallas)	SM 129	—	1	—
	SM 131	1	1	—
	SM 185	1 (1)	—	—
* <i>Megerlia acurra</i> sp. nov.	SM 255	1 (1)	—	—
	SM 239	2 (2)	—	—
<i>Megerlina pisum</i> (Lamarck)	SM 163	1	—	—
	SM 179	1 (1)	—	—
	SM 180	1	—	—
	SM 185	7 (7)	2	2

Family Phaneroporidae

* <i>Leptothyrella</i> cf. <i>ignota</i> (Muir-Wood)	SM 129	1	—	—
--	--------	---	---	---

* New records for South African waters

** Number of live specimens shown in brackets

BRACHIOPOD DISTRIBUTION

As reported by Cooper (1973b, 1973c), Recent brachiopods are commonly thought of as rare animals and while it is true they are greatly outnumbered by molluscs in the world's oceans, they are more widely distributed and in greater variety than previously suspected. In the last 20 years research cruises by a number of vessels from different countries have added considerably to our understanding of modern-day brachiopod distribution. They are known from all parts of the world and in some places form the major elements in the invertebrate macrofauna (Cooper 1973c: 1).

On a local scale, the cruises of the *Meiring Naude* have added substantially to the knowledge of the brachiopod fauna off the South African coast. In the cruises from 1975 to 1979 the vessel has collected 17 species belonging to 13 genera, 8 of the species recorded for the first time from South African waters.

GEOGRAPHIC DISTRIBUTION

The brachiopod fauna from off the Natal and eastern Cape coast, as is to be expected, shows greatest affinity with other Indian Ocean faunas. Some species are known only from South African waters: *Agulhasia davidsoni*, *Kraussina rubra*, *Xenobrochus africanus* and *X. agulhasensis*, while others extend their range from other parts of the Indian Ocean: *Dyscolia johannisdavisi* from around the Maldiv Islands, *Chlidonophora chuni* from the Maldiv Islands and south of Madagascar, *Eucalathis fasciculata* from south of Madagascar, and *Leptothyrella ignota* from off Zanzibar and the Gulf of Aden—assuming the specimens of *Dyscolia* and *Leptothyrella* described herein are indeed conspecific with the forms mentioned. Two new species represent totally unexpected additions to the fauna: *Grammetaria africana* is the first record of the genus outside the Philippines and *Notozyga gracilis* is a new form of a genus previously only recorded from the Caribbean.

BATHYMETRIC DISTRIBUTION

It is generally believed that the greatest diversity of brachiopod species is to be found on the continental shelf areas, generally taken by geologists to extend down to the 200 m line. Zézina (1970) states that the overwhelming majority of brachiopods live at depths down to 500 m. If the figures of 200 m and 500 m are taken to divide the ocean into shallow, intermediate and deep zones, then it can be seen from Table 1 that by far the greatest number of specimens collected by the *Meiring Naude* came from waters more than 500 m deep, with only *Crania* sp. and the members of the Kraussinidae being essentially shallow-water forms. According to previous descriptions, this is to be expected for species such as *Dyscolia* cf. *johannisdavisi*, *Chlidonophora chuni*, *Eucalathis fasciculata* and *Leptothyrella* cf. *ignota*, again assuming that the South African specimens of *Dyscolia* and *Leptothyrella* are conspecific with the previously described forms. However, previous records of *Agulhasia davidsoni*, *Xenobrochus africanus* and *X. agulhasensis* suggest they are forms that live at shallow to intermediate depths. In the case of *A. davidsoni* the state of the shells suggests they have been moved from their living site and they may well have been carried by currents from shallower water. *Xenobrochus africanus* has previously been recorded only from Durban Bay at a depth of 366 m and since some of the specimens described herein were found live, these new records simply extend the range of the species into deeper water.

The single specimen of *X. agulhasensis* was recovered dead so it may well have been transported from shallower water, but it must be remembered that the

TABLE 1

Depth ranges of the brachiopod species collected during the *Meiring Naude* cruises 1975–1979.

Species	Shallow 0–200 m (8 stations)	Intermediate 200–500 m (4 stations)	Deep >500 m (35 stations)
<i>Crania</i> sp.	x		
<i>Grammetaria africana</i>			x
<i>Dyscolia</i> cf. <i>johannisdavisi</i>			x
<i>Xenobrochus africanus</i>			x
<i>Xenobrochus agulhasensis</i>			x
<i>Xenobrochus</i> sp. 1.			x
<i>Xenobrochus</i> sp. 2.			x
<i>Terebratulina</i> sp.	x		x
<i>Chlidonophora chuni</i>			x
<i>Notozyga gracilis</i>			x
<i>Notozyga</i> sp.			x
<i>Eucalathis fasciculata</i>			x
<i>Agulhasia davidsoni</i>			x
<i>Kraussina rubra</i>	x		x
<i>Megerlia acrua</i>	x		
<i>Megerlina pisum</i>	x		
<i>Leptothyrella</i> cf. <i>ignota</i>			x

continental shelf off the east coast of South Africa is very narrow with a steep continental slope and this may well have a bearing on the bathymetric distribution of the brachiopods. Certainly the previous records of *X. agulhasensis* are from shallow and intermediate waters off the Cape of Good Hope, and on the Agulhas Bank where the continental shelf is much broader.

SYSTEMATIC ACCOUNT

Most of the genera recorded here belong to the superfamilies Terebratulacea and Cancellothyridacea of the suborder Terebratulidina. The classification schemes employed herein for these two superfamilies are those proposed by Cooper (1973a) for the Cancellothyridacea and Cooper (1983) for the Terebratulacea. Otherwise the classification is that used by Williams *et al.* (1965) in the *Treatise on invertebrate paleontology*.

Class INARTICULATA Huxley, 1869

Order ACROTRETIDA Kuhn, 1949

Suborder CRANIIDINA Waagen, 1885

Superfamily CRANIACEA Menke, 1828

Family **Craniidae** Menke, 1828

Genus *Crania* Retzius, 1781

Crania sp.

Fig. 2

Material

A single live specimen (SAM-A25445) found attached to *Megerlia accura* sp. nov. from SM 239 at a depth of 90 m.

Description

Small elongately oval shell with conical profile; apex low, about one-third of valve length from posterior margin. Posterior slope gently convex; anterior slope

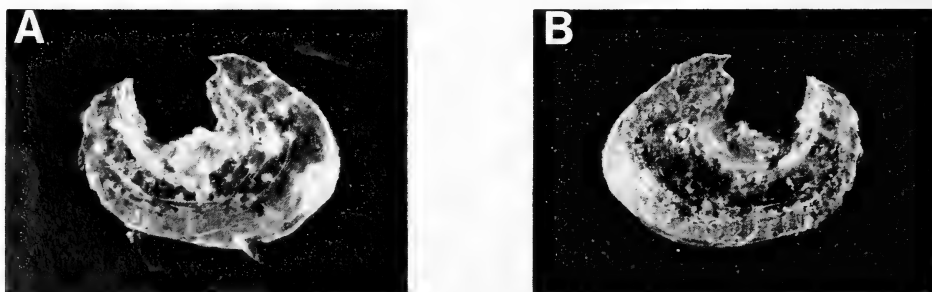


Fig. 2. *Crania* sp., SAM-A25445, SM 239. A. Ventral valve exterior, ventral view. B. Dorsal valve exterior, dorsal view. Both $\times 8$. The specimen is damaged.

gently convex near apex, becoming concave towards margin. Shell substance very thin; ornamented by concentric growth lines.

Ventral valve concave from attachment to convex surface and pitted where it covered tubercles on surface of pedicle valve of *Megerlia acrura*.

Details of interiors of both valves obscure except for pustules on inside of ventral valve corresponding to pits on outer surface.

Dimensions (mm)

	<i>Length</i>	<i>Width</i>
SAM-A25445	c. 4	c. 3

Discussion

Previous descriptions of *Crania*, such as that by Thomson (1927: 135), show it to be a genus that displays considerable variation among its assigned species, many of which are inadequately defined, a point made by Cooper (1973c: 19) in his description of *C. patagonica* Dall. The nearest species of *Crania* to that described here is *C. roseoradiata* Jackson, which is recorded from off the Cape west coast, although Turton (1932: 260) records a shell that may doubtfully be assigned to *Crania* from Port Alfred on the east coast. The present specimen was damaged during recovery and the shell substance is so thin (although calcified) that it offers no details of the internal structures that may be used in comparisons with other species. Certainly, the specimen lacks the radiating rose-coloured streaks that are said to distinguish Jackson's species, although colour is not a good criterion on which to define species. More and better-preserved specimens are required before this one can be named.

Class ARTICULATA Huxley, 1869
 Order RHYNCHONELLIDA Kuhn, 1949
 Superfamily RHYNCHONELLACEA Gray, 1848
 Family **Frieleidae** Cooper, 1959
 Genus *Grammetaria* Cooper, 1959
Grammetaria africana sp. nov.

Fig. 3

Diagnosis

Triangular *Grammetaria* with straight anterior margin parallel to hinge line; ventral umbo sharply pointed, nearly straight; radial ornament only faintly developed.

Material

Holotype. SAM-A25446 in the South African Museum, Cape Town. From SM 232 (32°14,9'S 20°10,4'E) at a depth of 560–620 m, 25 June 1979. The sole

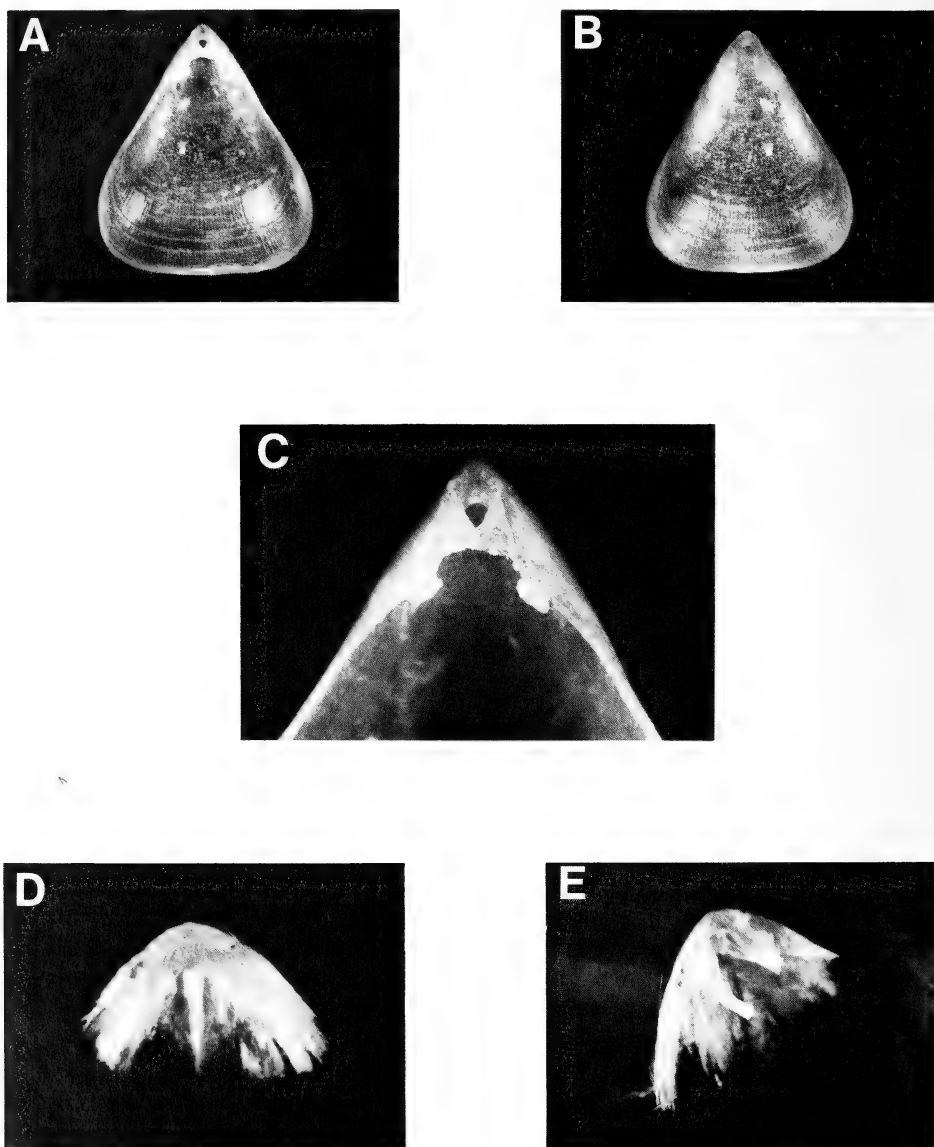


Fig. 3. *Grammetaria africana* sp. nov., SAM-A25446, holotype, SM 232. A-B. Internal and external views of pedicle valve. C. Close-up of ventral beak, dorsal view, showing auriculate deltidial plates. D-E. Ventral and lateral views of cardinalia. A-B $\times 3$. C-E $\times 8$. The brachial valve is damaged.

specimen was live when collected, being attached by a short slender pedicle to a small pebble.

Description

Elongate triangular outline with maximum width close to anterior margin. Valves convex with pedicle valve slightly deeper than brachial. Anterior commissure rectimarginate. Pedicle valve with evenly convex lateral profile; anterior profile gently convex in central portion between almost flat, steeply sloping flanks. Beak small, pointed, nearly straight. Foramen small, elongately oval, hypothrydid; deltidial plates auriculate, conjunct. Ornament of faintly developed capillae and concentric growth rings.

Pedicle valve interior with small corrugated teeth, supported by strong vertical dental plates. Pedicle collar well developed, free anteriorly.

Brachial valve interior with corrugated sockets bounded by strong socket ridges. Crura short, curved, of spinulifer type, triangular in cross-section but becoming flattened, blade-like distally. Outer hinge plates very narrow; inner hinge plates fused medianly to plug of shell material that occupies space bounded by median septum and crural bases. Median ridge thick, supporting proximal ends of crural bases.

Dimensions (mm)

		<i>Length</i>	<i>Width</i>
SAM-A25446	Holotype	10,9	9,3

Discussion

Grammetaria is characterized by its rectimarginate anterior commissure and its auriculate and conjunct deltidial plates. Possession of these features allows the present specimen to be referred immediately to that rare genus.

The only other species thus far assigned to the genus is *G. bartschi* (Dall), which is represented by only two specimens recovered from Philippine waters (Cooper 1959: 58) and a fragmentary specimen from off Bali (Zezina 1981: 12). They show some differences with that described here and are therefore taken to belong to a separate species. The anterior margin of the South African shell is not curved like that of *G. bartschi* but is remarkably straight and parallel to the hinge axis. The beak is much more pointed and nearly straight rather than suberect, and the radial ornament is much less strongly developed.

The exact relationships between these two species cannot be properly assessed on so few specimens. When more material becomes available it might be possible to take into account the full range of variation but until that time it is felt that sufficient differences exist between the South African and Philippine specimens for them to be regarded as separate species.

Etymology

The specific name alludes to the fact that this is the first record of the genus from African waters.

Order TEREBRATULIDA Waagen, 1883
Suborder TEREBRATULIDINA Waagen, 1883
Superfamily TEREBRATULACEA Gray, 1840
Family **Dyscoliidae** Fischer & Oehlert, 1891
Subfamily Dyscoliinae Fischer & Oehlert, 1891
Genus *Dyscolia* Fischer & Oehlert, 1890
Dyscolia cf. *johannisdavisi* (Alcock, 1894)

Figs 4–5

Terebratula johannisdavisi Alcock, 1894: 139. Blochmann, 1908: 638.

Terebratula wyvillei Davidson: Thomson, 1927: 201 (in part).

Dyscolia johannisdavisi (Alcock): Helmcke, 1940: 261, figs 22, 25b. Muir-Wood, 1959: 300, pl. 1 (figs 1, 3, 4).

Material

Four pairs of conjoined valves, one live at time of collection, plus a brachial and two pedicle valves (SAM-A25447 to A25453) all from SM 174 at a depth of 760 m.

Description

Large, roundedly triangular to elongately oval shells; biconvex with maximum width at midvalve or anterior to midvalve. Lateral and anterior margins of largest specimens strongly incurved (flanged); anterior commissure rectimarginate. Beak short, truncated, suberect to erect; foramen large, subcircular, permesothyridid to epithyridid, labiate. Symphytium concave, almost completely hidden by dorsal beak. Shell substance thick in large specimens; surface marked by concentric growth lines and very faint radial capillae.

Pedicle valve fairly evenly convex in lateral profile; anterior profile variably convex, often strongly domed with steep flanks. Brachial valve moderately to strongly convex in lateral profile; gently domed in anterior profile. Greatest convexity in umbonal region with posterolateral corners slightly flattened.

Ventral interior with stout teeth not supported by dental plates and short elevated pedicle collar. Muscle scar subrectangular; adductor scar occupies about one-third of total width of scar. Dorsal interior with strong high socket ridges bounding wide shallow sockets. Fulcral plates thick and extended laterally into broad shelves. Cardinal process transversely elliptical, about one-tenth as wide as valve, often roughened and pitted posteriorly; extends over posterior ends of socket ridges. Outer hinge plates narrow, concave, indistinct. Loop preserved only in two specimens. In the large specimen the crura are short rounded extensions of the socket ridges and merge, at about midloop, with descending lamellae without development of crural processes. In the smaller specimen the crura are curved and flattened and united with descending lamellae anterior of midloop with development of short, blunt crural processes. In both specimens,

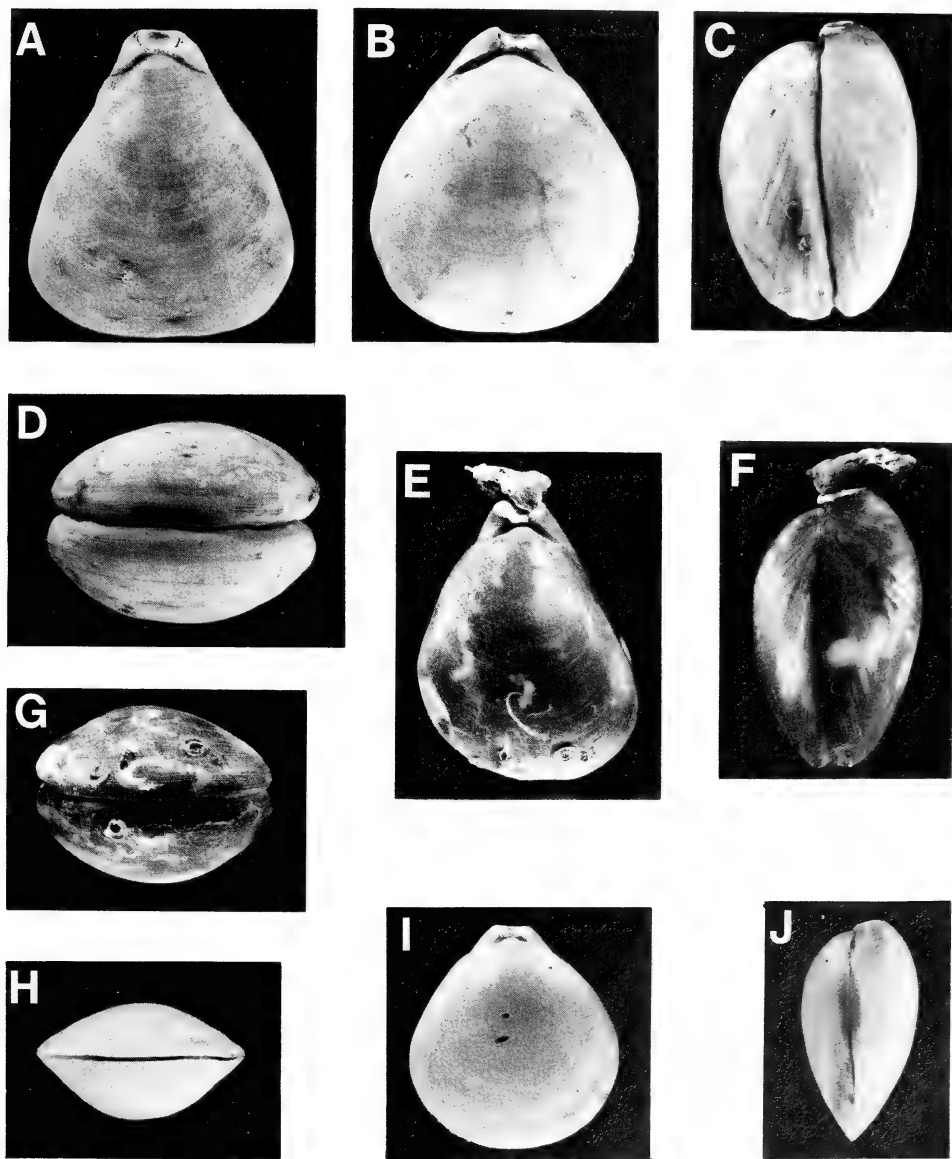


Fig. 4. *Dyscolia* cf. *johannisdavisi* (Alcock, 1894), SM 174. A. SAM-A25447: dorsal view of conjoined valves. B-D. SAM-A25448: dorsal, lateral and anterior views of conjoined valves. E-G. SAM-A25449: dorsal, lateral and anterior views of conjoined valves with pedicle and serpulid worm tubes. H-J. SAM-A25453: anterior, dorsal and lateral views of conjoined valves. All $\times 1$.

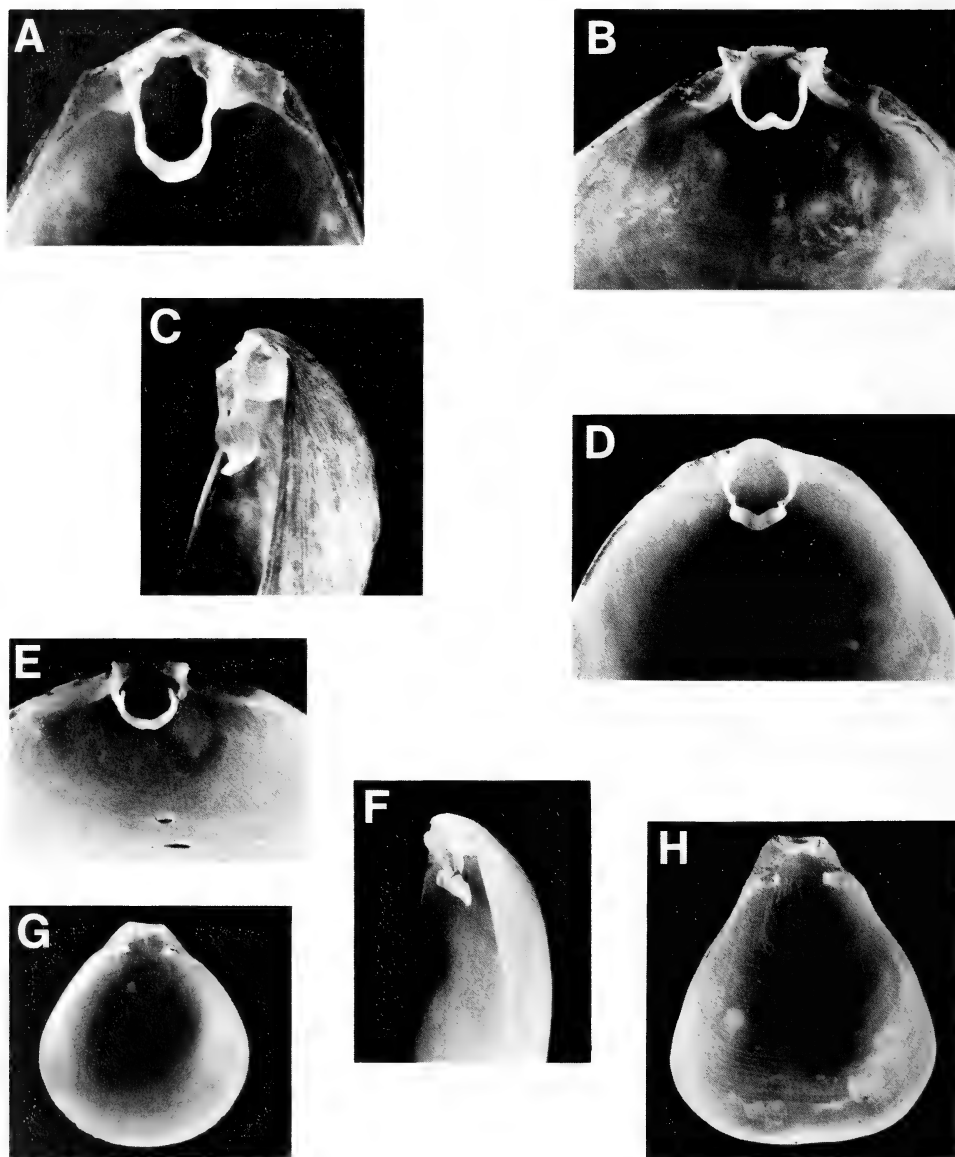


Fig. 5. *Dyscolia* cf. *johannisdavisi* (Alcock, 1894), SM 174. A-C. SAM-A25449: ventral, anterior and lateral views of loop. D-F. SAM-A25453: ventral, anterior and lateral views of loop. G. SAM-A25453: interior view of pedicle valve. H. SAM-A25447: interior view of pedicle valve showing muscle scars. A-F $\times 2$. G-H $\times 1$.

descending lamellae and transverse bands are broad with the latter bearing low median folds that are extended anteriorly as blunt points. Muscle field subquadrate.

Dimensions (mm)

	<i>Length</i>	<i>Width</i>	<i>Thickness</i>	Brachial valve	<i>Apical</i>
				<i>Length</i>	<i>angle</i>
SAM-A25447	41,8	35,7	26,6	39,6	50°
A25448	41,3	37,5	27,8	38,8	84°
A25449	41,1	32,8	24,9	37,3	59°
A25450	34,9	28,2	—	—	62°
A25451	35,8	28,2	—	—	—
A25452	—	32,7	—	33,4	—
A25453	29,9	28,1	11,0	28,6	79°

Muscle field dimensions (mm)

	Pedicle valve		Brachial valve	
	<i>Length</i>	<i>Width</i>	<i>Length</i>	<i>Width</i>
SAM-A25447	16,7	9,0	9,8	9,5
A25448	20,7	11,6	11,1	11,9
A25450	15,4	8,1	—	—
A25452	—	—	11,2	11,7
A25453	10,6	7,3	—	—

Loop dimensions (mm)

	<i>Length</i>	<i>Width</i>
SAM-A25449	10,5	4,9
A25453	6,4	3,9

Discussion

The small sample of *Dyscolia* described here from a single locality shows considerable morphological variation, which makes its assignment to one of the known species of *Dyscolia* difficult. The specimens show differences and similarities with most of the described species, e.g. the large size and triangular outline are reminiscent of *D. wyvillei* (Davidson) and *D. johannisdavisi* (Alcock), while the subcircular outline of the smallest specimen is more like those of *D.?* *radiata* Cooper and *D. ewingi* Cooper. However, *D. ewingi* has now been removed from *Dyscolia* to become the type-species of the new genus *Gonio-brochus* (Cooper 1983: 261). The broad transverse band of the present specimens differs from those of *D. wyvillei* and *D. johannisdavisi*, which are said to be thin

and delicate (Cooper 1973c: 19; 1983: 254), but it is like that of the fossil *D. guiscardiana* (Seguenza) from the Pliocene of Sicily. *Dyscolia johannisdavis* and *D. ? radiata* are both recorded from the Indian Ocean, but the latter differs in the form of its loop.

The author has examined the holotype of *D. wyvillei* and a brachial valve of *D. johannisdavis* in the British Museum (Natural History). These two forms are closely similar and Muir-Wood (1959: 301) reports that although some authors would wish to synonymize them (e.g. Thomson 1927: 201), there are differences that are probably sufficient to separate the species. As pointed out by Muir-Wood (1959), *D. wyvillei* has a longer, more narrowly tapering ventral umbo, a longer, better-exposed symphytium and more strongly developed radial ornament. *Dyscolia johannisdavis* has a more marked marginal flange, a short concave symphytium that is usually hidden by the dorsal umbo and only faintly developed radial ornament. Indeed, in Alcock's original description (1894: 139) no mention is made of any radial ornament. Helmcke (1940: 267) regards the hinge plates of the two forms to be different; those of *D. wyvillei* are large, wide, almost square, while those of *D. johannisdavis* are small, narrow and barely developed. The holotype of *D. wyvillei* has a row of denticles around the interior margin of both valves. No such feature has been described from *D. johannisdavis* nor are any denticles visible on any of the South African specimens.

Of the two species, the South African shells described here are undoubtedly closer to *D. johannisdavis*, the main difference being in the form of the loop. Cooper (1983) attaches considerable taxonomic importance to the form of the loop, using it to distinguish between species and genera of terebratulaceans. However, in view of the amount of variation in other characters of the shell displayed by the *Meiring Naude* sample, it is felt that similar variation may be seen in the form of the loop, and erection of a new taxon is unwarranted at this stage.

Subfamily Aenigmathyridinae Cooper, 1983

Genus *Xenobrochus* Cooper, 1981

The classification and identification of terebratulacean brachiopods depends, to a large extent, on the form of the loop and its relative proportions. Cooper (1983) has established a number of new families, subfamilies, genera and species based largely on this character of the shell. However, placing such taxonomic importance on a single feature raises several problems, especially when what appear to be minor differences are used to distinguish between genera. Most species of Recent Terebratulacea, particularly those from fairly deep water, are established on only a few specimens at most. Thus, the limits of loop variation in a single population or species are still virtually unknown, although for some species such as *Liothyrella neozelanica* and, as has been shown, *Dyscolia* cf. *johannisdavis* it is obvious that considerable variation may be present.

Further problems are encountered with the identification of juveniles of short-looped genera when only the adult loop has been described, and specimens

in which the loop has not been completely preserved are especially difficult to classify. Two such forms are present in the *Meiring Naude* material. However, other features of the shells, such as their small to medium size, lack of radial ornament, rectimarginate anterior commissures, narrow crura and poorly defined outer hinge plates, suggest they belong to the subfamily Aenigmathyridinae Cooper, 1983. Recent members of this subfamily include *Abyssothyris*, *Acrobelesia* and *Xenobrochus*, and of these *Xenobrochus* probably best accommodates the specimens described below and it is to this genus that they are tentatively assigned.

Xenobrochus africanus (Cooper, 1973)

Fig. 6

Gryphus africanus Cooper 1973b: 8, pl. 4 (figs 31–38).

Xenobrochus africanus (Cooper) Cooper, 1981: 20, pl. 4 (figs 30–35).

Material

Thirteen complete specimens and a single pedicle valve (SAM-A25454) from SM 103 at a depth of 680 m; one complete specimen (SAM-A25455) from SM 129 at a depth of 850 m; a single brachial and three pedicle valves (SAM-A25456) from SM 131 at a depth of 780 m; a damaged pedicle valve (SAM-A25457) from SM 162 at a depth of 630 m. Most of the complete specimens were live at the time of collection, some attached to small pebbles by short slender pedicles.

Description

Small biconvex shells with elongately oval outline. Anterior commissure rectimarginate; beak small, suberect; foramen mesothyridid; deltidial plates conjunct forming completely visible symphytium. Shell surface smooth except for concentric growth lines.

Pedicle valve quite strongly and evenly convex in lateral profile; anterior profile strongly convex with evenly convex middle portion flanked by short steep sides. Brachial valve subcircular with evenly and gently convex lateral profile; anterior profile strongly convex with narrow median portion bounded by flatter sides.

Ventral interior with strong teeth not supported by dental plates or thickened valve wall; pedicle collar short, excavate anteriorly. Details of muscle scars not visible. Dorsal interior with high socket ridges bounding deep sockets; outer hinge plates narrow, concave and tapering anteriorly to join thin crural bases. Crura narrow, bearing scoop-like anterior part of loop without development of descending lamellae. Crural processes low and blunt and attached directly to narrow transverse band, which is convex dorsally and anteriorly.

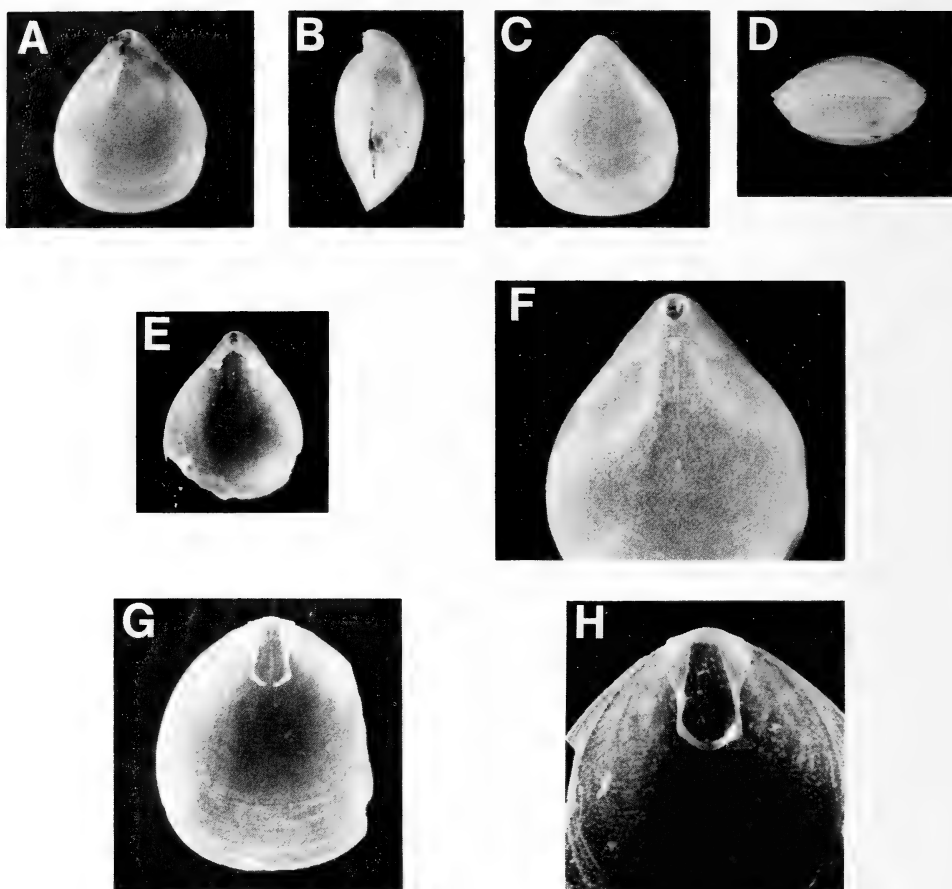


Fig. 6. *Xenobrochus africanus* (Cooper, 1973). A-D. SAM-A25454, SM 103: dorsal, lateral, ventral and anterior views of conjoined valves with pedicle. E. SAM-A25454, SM 103: interior view of pedicle valve. F. SAM-A25455, SM 129: dorsal view of conjoined valves. G. SAM-A25454, SM 103: interior view of brachial valve. H. SAM-A25454, SM 103: ventral view of loop. A-E $\times 3$. F-G $\times 6$. H $\times 8$.

Dimensions (mm)

	<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SAM-A25454	3,8	3,5	1,8
	6,6	5,1	3,4
A25455	6,1	5,2	3,0
A25456	6,6	5,9	—
A25457	—	5,2	—

Loop dimensions (mm)

	<i>Length</i>	<i>Width</i>
SAM-A25454	1,5	0,7

Discussion

This genus is characterized by its small size, rectimarginate anterior commissure and a loop that has a transverse band convex toward the anterior (Cooper 1983: 275). Of the species assigned to the genus, *X. indianensis* (Cooper), *X. australis* Cooper, *X. anomalus* Cooper and *X. africanus* (Cooper) bear the closest resemblance to the present specimens. Of these, *X. africanus* is recorded from the same area as these specimens but from shallower depths (Cooper 1973b: 3) and is so similar in morphology that the two forms must be regarded as being conspecific. The other species can be distinguished principally by their larger size but *X. indianensis* has a more incurved beak with partly concealed symphytium, fairly large cardinal process and narrow median fold on the transverse band of the loop. *Xenobrochus australis* is narrower and has an angular transverse band; *X. anomalus* is distinguished by its tubular pedicle collar.

Xenobrochus agulhasensis (Helmcke, 1938)

Fig. 7

Terebratula vitrea var. *minor* Philippi: Davidson, 1880: 29, pl. 2 (figs 5–6).

Liothyrida (*Gryphus*) sp. Blochmann, 1908: 613, pl. 39 (fig. 31).

Liothyrida agulhasensis Helmcke, 1938: 243; 1940: 258, fig. 21.

Material

A single complete dead specimen (SAM-A25458) from SM 232, at a depth of 560–620 m.

Description

Elongately oval, biconvex shells with rectimarginate anterior commissure; beak small, suberect with submesothyridid subcircular foramen. Deltidial plates conjunct forming short symphytium. Shell surface smooth except for concentric growth lines.

Pedicle valve quite strongly convex in both profiles. Brachial valve subcircular, over nine-tenths as long as pedicle valve, with gently convex profiles.

Ventral interior with small teeth not supported by dental plates; pedicle collar very short, excavate. Details of muscle scars not visible. Dorsal interior with quite low straight socket ridges bounding fairly wide sockets. Cardinal process transversely elliptical, covering posterior ends of socket ridges. Outer hinge plates narrow, triangular and tapering anteriorly to merge with crural bases. Crura strong, rounded in section, bearing anterior part of loop, which is convex anterodorsally. Crural processes small blunt points in midloop position and attached directly to broad transverse band, which bears faint ventrally directed median fold.

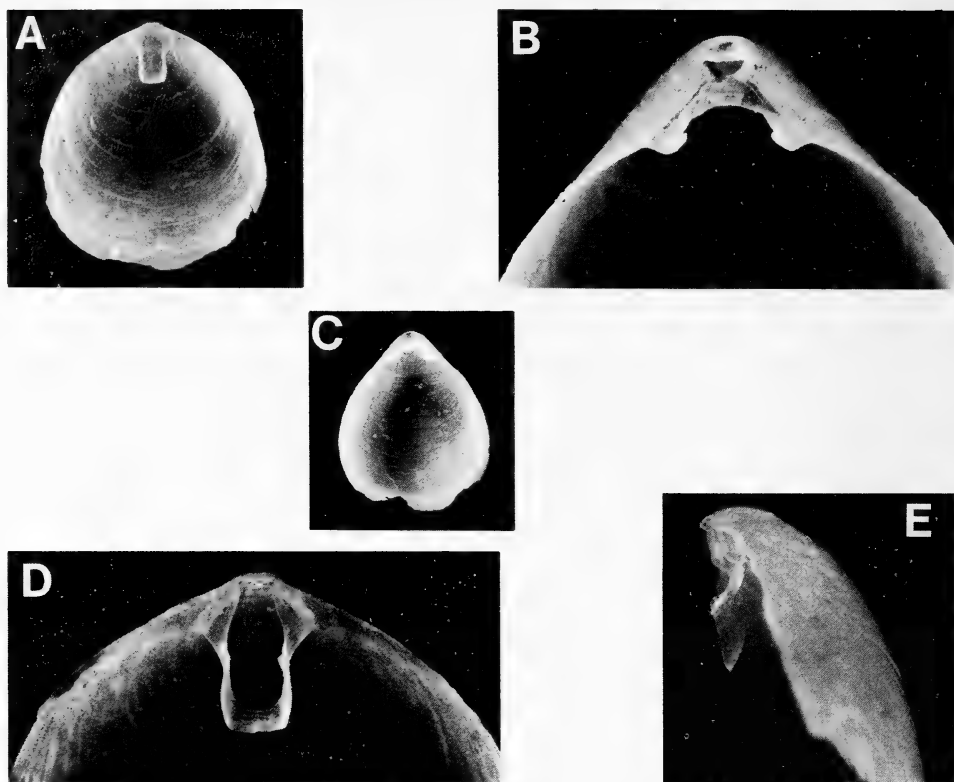


Fig. 7. *Xenobrochus agulhasensis* (Helmcke, 1938), SAM-A25458, SM 232. A. Interior view of brachial valve. B. Close-up of ventral beak, dorsal view. C. Interior view of pedicle valve. D-E. Ventral and lateral views of loop. A $\times 3$. B, D-E $\times 8$. C $\times 2$.

Dimensions (mm)

	<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SAM-A25458	11,7	9,9	6,7

Loop dimensions (mm)

	<i>Length</i>	<i>Width</i>
SAM-A25458	2,1	1,2

Discussion

This specimen bears a close resemblance to *Liothyryna agulhasensis* Helmcke from the Agulhas Bank. The species was first described by Davidson (1880) after two specimens were dredged off the Cape of Good Hope during the *Challenger* Expedition. Davidson identified the specimens as *Terebratula vitrea* var. *minor*

Philippi, which is synonymous with *Liothyrella affinis* Calcara. The author has examined one of Davidson's specimens in the British Museum (Natural History) and found it to be very similar to that described here, particular in the form of the loop.

Further specimens from the Agulhas Bank were recovered by the *Valdivia* Expedition in 1898. Blochmann (1906, 1908) compared these to Davidson's specimens and concluded that both were separable from *L. affinis* on the grounds that their loops were different. He assigned the specimens to *Liothyrina* (*Gryphus*) but left the species unnamed. The loop figured by Blochmann (1908, pl. 39 (fig. 31)) is very similar to that of the specimen described here.

Helmcke (1940: 258) revised Blochmann's descriptions and again emphasized the differences between the loops of *L. agulhasensis* and *L. affinis*, that of the former being more rounded while the latter had an angular transition between the transverse band and the sides of the loop. Helmcke described the transverse band of *L. agulhasensis* as being like a weakly fallen arch (? i.e. concave ventrally).

The present author follows Cooper (1981: 20, 1983: 275) in assigning the species to *Xenobrochus* because the transverse band of the loop is convex dorsally and anteriorly, a distinguishing characteristic of the genus.

Jackson (1952: 17) mentions the possibility that the 'Challenger' and 'Valdivia' specimens might belong to his *Gryphus capensis* but in his description of the loop of this species he states that the transverse band is narrow and arched ventrally. This would immediately separate *G. capensis* from any of the specimens mentioned here and indeed exclude it from *Xenobrochus*. Also the thread-like median septum separating adductor scars in the brachial valve of *G. capensis* is a feature not seen in any species of *Xenobrochus*.

It is interesting to note that Cooper (1983: 275) has now questionably assigned *Liothyrella affinis* to *Xenobrochus*.

Xenobrochus? sp. 1

Fig. 8

Material

One complete dead specimen (SAM-A25459) from SM 131 at a depth of 780 m.

Description

Small, elongately oval biconvex shell with maximum width about midvalve; anterior commissure rectimarginate. Beak moderately long, narrowly rounded, suberect to erect; foramen large, mesothyridid. Deltidial plates disjunct or conjunct; symphytium short, visible. Shell surface smooth but for concentric growth lines.

Pedicle valve deeper and more convex than brachial valve, evenly convex in lateral profile, strongly convex in anterior profile, especially in median portion.

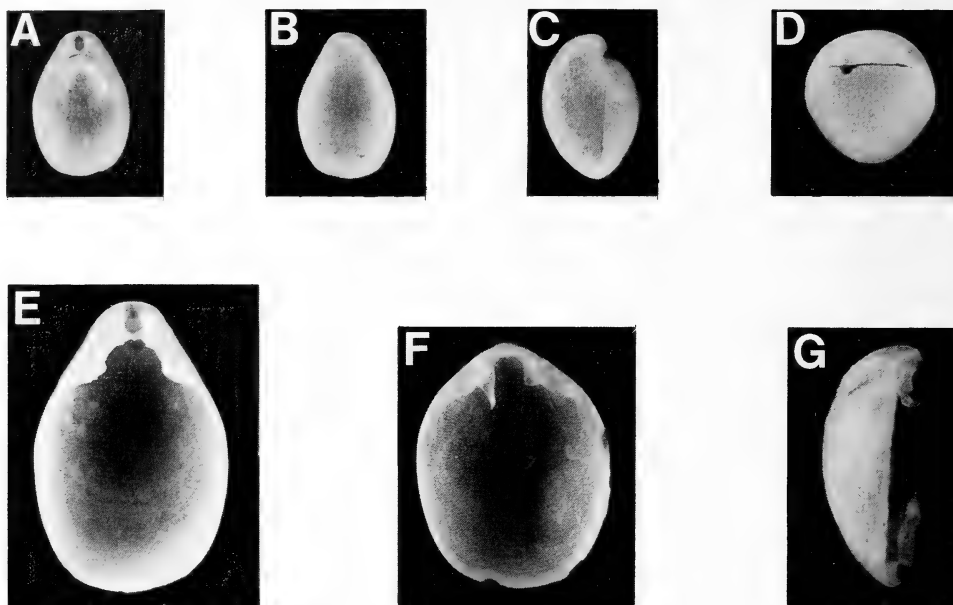


Fig. 8. *Xenobrochus?* sp. 1, SAM-A25459, SM 131. A-D. Dorsal, ventral, lateral and anterior views of conjoined valves. E. Interior view of pedicle valve. F. Interior view of brachial valve. G. Lateral view of brachial valve showing crus. A-D $\times 3$. E-G $\times 6$.

Brachial valve moderately convex in lateral profile, more strongly convex in anterior profile.

Ventral interior with strong teeth; pedicle collar excavate anteriorly. Details of muscle scars not discernible. Dorsal interior with broad, transversely elliptical cardinal process extending across posterior ends of socket ridges; socket ridges high posteriorly but lower at their anterior ends, bounding narrow sockets. Outer hinge plates flattish, tapering anteriorly and merging with crural bases. Crura thin, subparallel; crural processes very small. Remainder of loop not preserved.

Dimensions (mm)

	<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SAM-A25459	6,3	4,3	4,4

Discussion

This specimen bears a strong resemblance to *Xenobrochus anomalus* Cooper from the waters around Marion Island. However, that species is characterized by its extravagantly developed tubular pedicle collar and its crural processes are situated at the anterior limit of the outer hinge plates (Cooper 1981: 20). While the present specimen has a well-defined pedicle collar, it could hardly be

described as extravagant and the crural processes are located anterior of the outer hinge plates.

Xenobrochus? sp. 2

Fig. 9

Material

Six pedicle and three brachial valves (SAM-A25460) from SM 232 at a depth of 560–620 m and a pedicle and brachial valve (SAM-A25461) from SM 226 at a depth of 710–775 m.

Description

Small to medium elongately oval shells with maximum width at or slightly anterior of midvalve; anterior commissure rectimarginate. Beak moderately long, quite narrowly rounded, suberect to erect; foramen quite large, mesothyridid; symphytium short, visible. Shell surface smooth except for concentric growth lines.

Pedicle valve deeper and more convex than brachial valve; moderately convex in lateral profile with maximum convexity in umbonal region; strongly convex in anterior profile. Brachial valve gently and evenly convex in both profiles.

Ventral interior with small elongate teeth; pedicle collar short, excavate anteriorly. Muscle scars not visible. Dorsal interior with transversely elliptical cardinal process; high socket ridges bounding fairly wide sockets; outer hinge plates small, merging with crural bases. Crura thin; crural processes small, blunt. Remainder of loop not preserved. Lightly impressed elongate rectangular muscle scars, extending for about one-third of the valve length, barely discernible beneath loop.

Dimensions (mm)

	<i>Length</i>	<i>Width</i>
SAM-A25460	14,7	11,1
	13,7	10,5
	13,3	9,9
	11,8	9,2
SAM-A25461	11,7	8,4

Discussion

These specimens resemble *Xenobrochus indianensis* (Cooper) from the north-western part of the Indian Ocean, although without a complete loop further comparison is impossible.

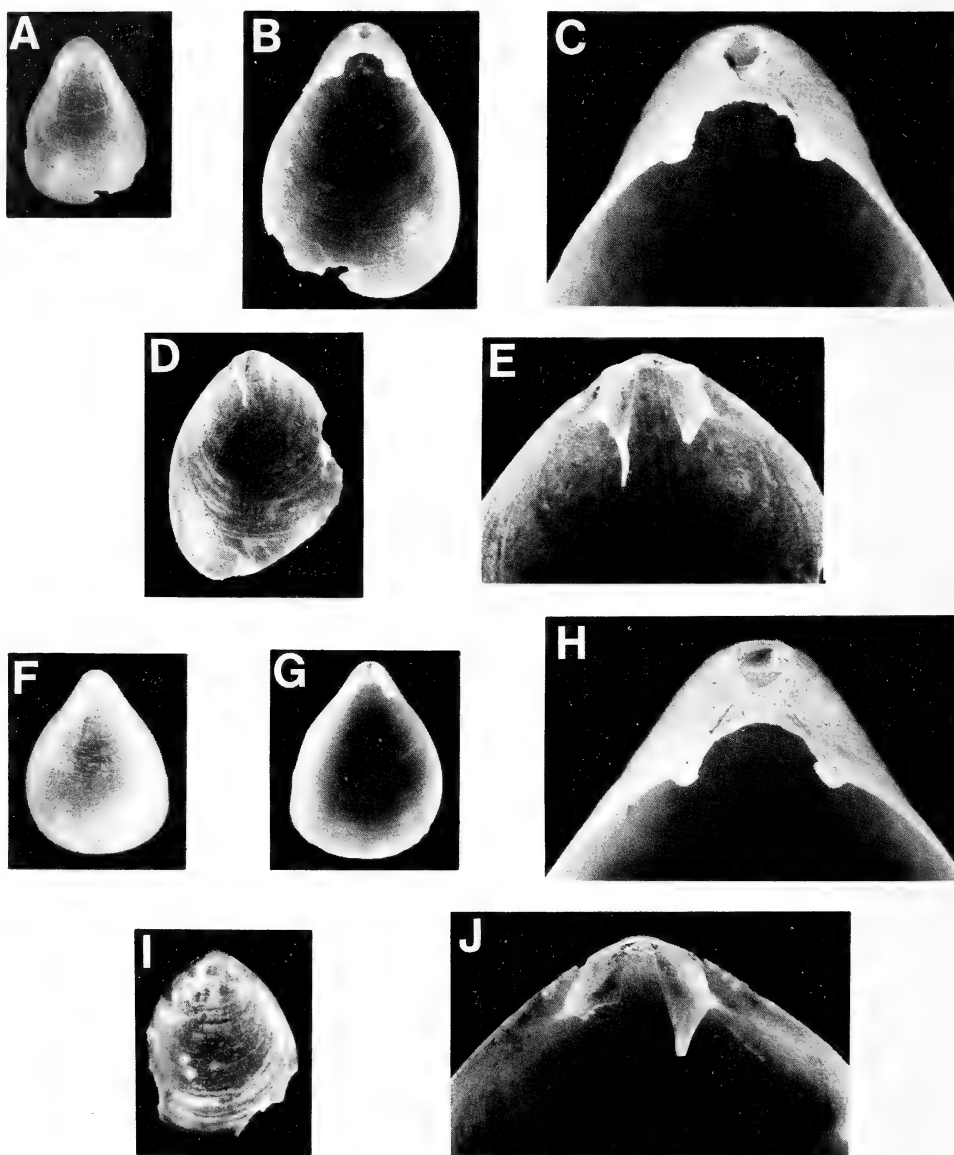


Fig. 9. *Xenobrochus?* sp. 2. A-E. SAM-A25461, SM 226. A. Ventral view of pedicle valve. B. Interior view of pedicle valve. C. Close-up of ventral beak. D. Interior view of brachial valve. E. Close-up of cardinalia. F-J. SAM-A25460, SM 232. F. Ventral view of pedicle valve. G. Interior view of pedicle valve. H. Close-up of ventral beak. I. Dorsal view of brachial valve. J. Close-up of cardinalia. A, F, G, I $\times 2$. B, D $\times 3$. C, E, H, J $\times 8$.

Superfamily CANCELLOTHYRIDACEA Thomson, 1926

Family **Cancellothyrididae** Thomson, 1926

Subfamily Cancellothyridinae Thomson, 1926

Genus *Terebratulina* d'Orbigny, 1847

Terebratulina sp.

Fig. 10

Material

A total of 13 immature specimens: 8 complete specimens, 3 brachial valves and a pedicle valve (SAM-A25462) from SM 131 at a depth of 780 m, and a single complete specimen (SAM-A25463) from SM 180 at a depth of 80 m. All were dead at time of recovery.

Description

Very small biconvex shells with elongately oval to roundedly triangular outline; maximum width in anterior third of shell. Beak nearly straight with large submesothyridid foramen; deltidial plates very small. Anterior commissure rectimarginate. Ornament consisting of rounded costae and costellae and strong concentric growth lines. Many of the specimens have strongly beaded appearance caused by interference of radial and concentric ornaments. Posterolateral extremities with concentric ornament only.

Pedicle valve moderately convex in lateral profile; gently convex in anterior profile but with steep posterolateral slopes. Brachial valve gently convex in both profiles, but more arched umbonally. Posterolateral corners flattened.

Ventral interior with small hook-like teeth; pedicle collar short, excavate. Other details obscure. Dorsal interior with high, strong, widely divergent socket ridges fused posteriorly to weakly developed cardinal process; sockets short and deep. Crura short, stout, rounded in cross-section. Remainder of loop not preserved in any of these specimens.

Dimensions (mm)

	<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SAM-A25462	3,5	2,5	1,8
	3,2	2,3	1,5
	2,6	2,1	1,2
	2,3	1,9	1,1
SAM-A25463	4,2	3,5	2,0

Discussion

Terebratulina is very widespread in the world's oceans and is represented in South African waters by *T. abyssicola* (Adams & Reeve) and *T. meridionalis*

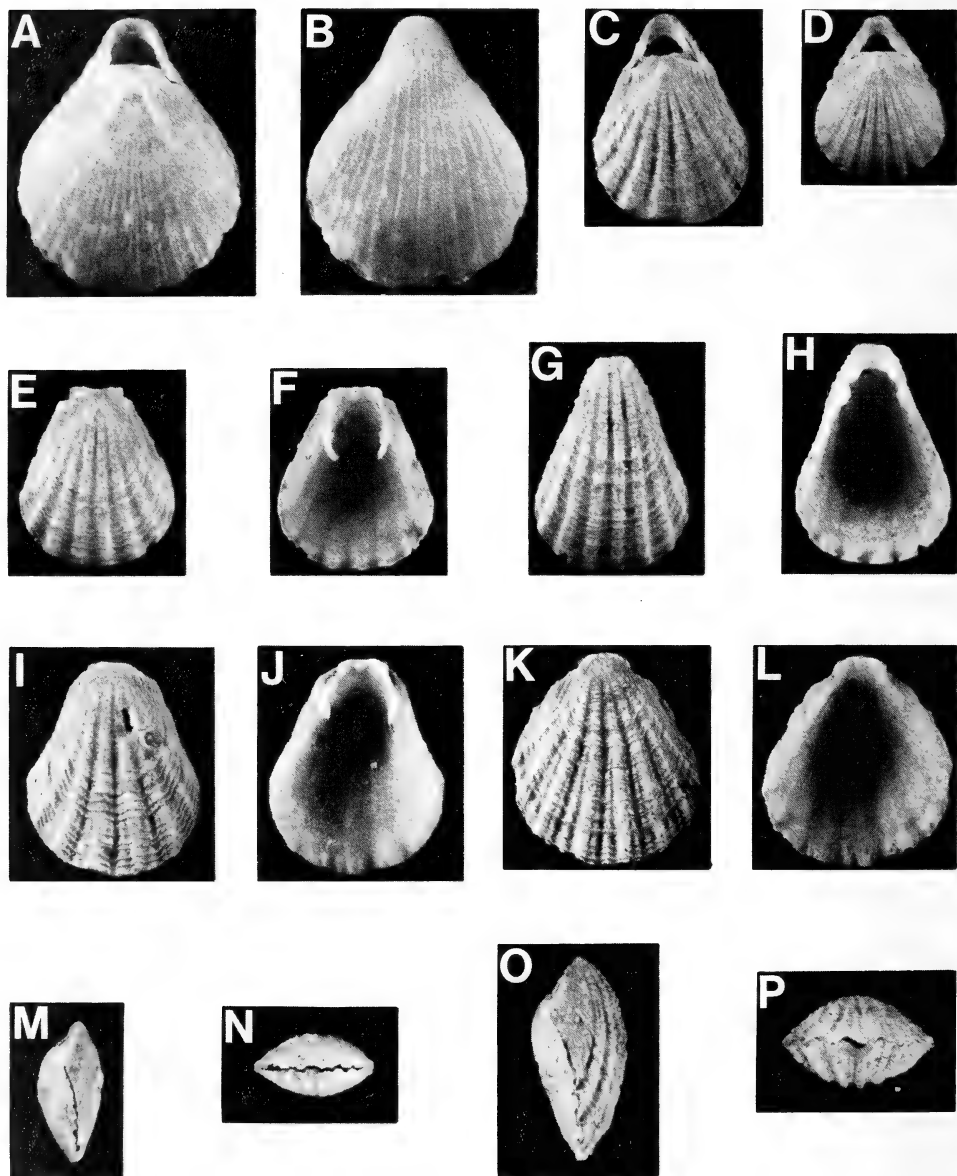


Fig. 10. *Terebratulina* sp. A-B. SAM-A25463, SM 180: dorsal and ventral views of conjoined valves. C-P. SAM-A25462, SM 131. C. Dorsal view of conjoined valves. D. Dorsal view of conjoined valves. E-F. Dorsal and interior views of brachial valve. G-H. Ventral and interior views of pedicle valve. I-J. Dorsal and interior views of brachial valve. K-L. Dorsal and interior views of brachial valve. M-N. Lateral and anterior views of conjoined valves. O-P. Lateral and anterior views of conjoined valves. All $\times 8$.

Jackson, as well as unnamed species recorded by Jackson (1952) and Cooper (1973b). The present specimens cannot be assigned to either of the above-named species because of their much stronger radial ornament. The beaded appearance of the ribs displayed by most of the present specimens is typical of many immature *Terebratulina* (Cooper 1978: 7) so until associated adult shells become available a more precise identification cannot be attempted. More than one species may be present in this sample.

Family **Chlidonophoridae** Muir-Wood, 1959
Subfamily Chlidonophorinae Muir-Wood, 1959
Genus *Chlidonophora* Dall, 1903
Chlidonophora chuni Blochmann, 1903

Fig. 11

Terebratula sp.: Alcock, 1894: 139.

Terebratulina sp.: Chun, 1900: 404, 405, 2 figs.

Chlidonophora chuni Blochmann in Chun, 1903: 435, 436, 2 figs. Blochmann, 1906: 695.

Thomson, 1927: 182. Helmcke, 1940: 239, fig. 6. Muir-Wood, 1959: 296, pl. 4 (figs 5–7).

Cooper, 1973b: 13, pl. 8 (figs 17–26).

Material

Two complete specimens (SAM–A25464), dead at time of recovery, from SM 103 at a depth of 680 m; three complete specimens (SAM–A25465), one dead and two live at time of recovery, from SM 246 at a depth of 1 640–1 660 m.

Description

Small subcircular biconvex shells with maximum width at about midvalve. Hinge line nearly straight, less than one-half as wide as valve. Anterior commissure broadly and very gently uniplicate. Beak short; interarea small; foramen hypothyridid; deltidial plates disjunct but one specimen with pedicle shows delthyrium closed anterior to pedicle by ?symphytium. Pedicle quite short, slender and frayed at end. Ornamentation of rounded costae and costellae crossed by strongly developed concentric growth lamellae to produce a reticulate pattern.

Pedicle valve gently convex in lateral profile; maximum convexity in umbonal region becoming flatter anteriorly. Anterior profile quite strongly arched with median flattening due to development of broad shallow sulcus originating near umbo. Brachial valve evenly convex in lateral profile; anterior profile arched by incipiently developed fold.

Pedicle valve interior with strong teeth but no dental plates; other details obscure. Brachial valve interior with short socket ridges fused posteriorly to transverse cardinal process; cardinalia project posterior to hinge line. Crura short, stout, converge anteromedianly, crural processes sharply pointed with points directed anteroventrally. Narrow transverse band with ventrally directed median fold.

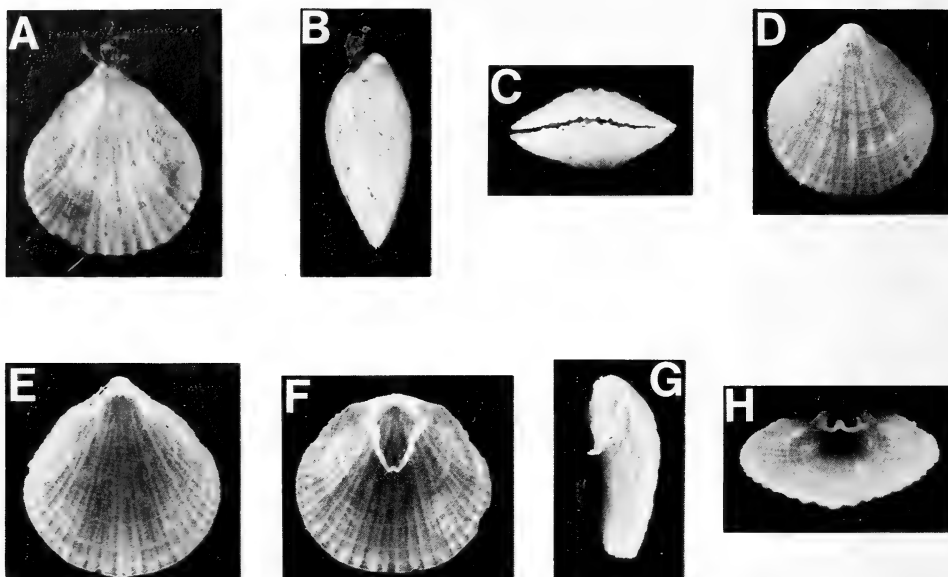


Fig. 11. *Chlidonophora chuni* Blochman, 1903, SAM-A25465, SM 246. A-B. Dorsal and lateral views of conjoined valves with pedicle. C. Anterior view of conjoined valves. D-E. Ventral and interior views of pedicle valve. F-H. Ventral, lateral and anterior views of brachial valve interior showing loop. All $\times 6$.

Dimensions (mm)

	<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SAM-A25464	4,7	4,1	2,2
	4,4	4,1	1,9
SAM-A25465	4,7	4,5	2,1
	4,1	3,9	1,9
	4,5	4,2	2,1

Loop dimensions (mm)

	<i>Length</i>	<i>Width</i>
SAM-A25465	1,9	0,9

Discussion

Two species of *Chlidonophora* are known; *C. incerta* (Davidson) from the Atlantic Ocean can be distinguished from *C. chuni* Blochmann from the Indian Ocean by the form of its pedicle, its loop and its wider hinge line. The pedicle of *C. chuni* is long and slender and frays some distance from the umbo whereas that of *C. incerta* frays immediately on emergence from the foramen to give a radiating effect. The loop of *C. chuni* is longer and more pointed than that of *C. incerta*, which is short and rounded. The *Meiring Naude* specimens have the

narrow hinge line and longer pointed loop of *C. chuni* and although the pedicle is not long it does not fray until a short distance from the umbo. They must therefore be placed in that species.

Genus *Notozyga* Cooper, 1977

Notozyga gracilis sp. nov.

Fig. 12

Diagnosis

Notozyga with subdued radial ornament and delicate, slender loop.

Material

Holotype. SAM-A25466 in the South African Museum, Cape Town. From SM 131 (30°43,2'S 30°40,8'E) at a depth of 780 m, 11 May 1977. One complete, dead specimen.

Description

Small biconvex shell with rounded subpentagonal outline; posterolateral angles obtuse. Hinge line straight, about two-thirds as wide as valve; maximum width slightly anterior of midvalve. Anterior commissure rectimarginate. Interarea quite high, about one-third as long as valve; foramen quite large, triangular, flanked by narrow deltidial plates. Well-defined triangular palintropes between deltidial plates and beak ridges. Ornament of very subdued rounded costae and costellae and very faint concentric growth lines.

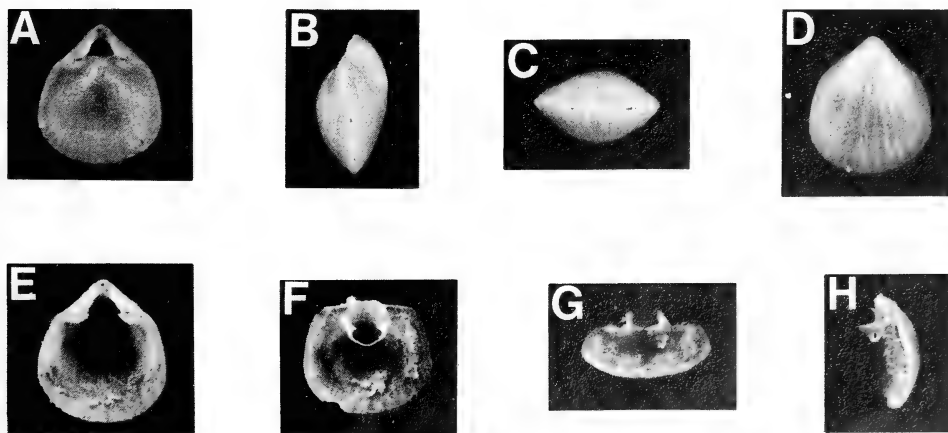


Fig. 12. *Notozyga gracilis* sp. nov., SAM-A25466, holotype, SM 131. A-D. Dorsal, lateral, anterior and ventral views of conjoined valves. E. Interior view of pedicle valve. F-H. Ventral, anterior and lateral views of brachial valve interior showing loop. All $\times 8$.

Pedicle valve lateral profile strongly convex near umbo, becoming less so anteriorly; anterior profile strongly convex. Brachial valve quite strongly convex in both profiles; posterolateral corners flattened.

Ventral interior with short, excavate pedicle collar; teeth strong, semicircular in shape, without dental plates. Dorsal interior with fairly high, widely divergent socket ridges, fused posteriorly and bounding narrow, deep sockets. Crura short, strong, projecting anteromedianly from below anterior ends of socket ridges. Crural processes moderately high, bluntly pointed. Descending lamellae very thin, curved, uniting medianly without development of true transverse band. Both valves with flattened rim around anterior and lateral margins with well-developed eminences and embayments inside this.

Dimensions (mm)

	<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SAM-A25466 Holotype	2,2	2,1	1,2

Loop dimensions (mm)

	<i>Length</i>	<i>Width</i>
SAM-A25466 Holotype	0,8	0,7

Discussion

The genus *Notozyga* is much like *Eucalathis* in appearance but can be distinguished principally by its well-defined ventral interarea and the rounded, as opposed to pointed, form of its loop, which extends only slightly beyond the crural processes (Cooper 1977: 105). The specimen described here possesses these distinctive features and is thus placed in that genus but it differs from the only previously described species, *N. lowenstami* Cooper, in its subdued ornament and finer, more delicate loop.

Eucalathis macrorhynchus Foster from the Pacific-Antarctic ridge is a form with a subdued radial ornament and well-defined interarea and in these respects resembles *N. gracilis*. The loops of these two species are also similar but in his description Foster (1974: 81) points out that *E. macrorhynchus* shows considerable variation in the form of its loop from rounded *Notozyga*-type to a more pointed shape typical of *Eucalathis*.

Another species worthy of investigation is *Eucalathis trigona* (Jeffreys), which Cooper (1973b: 13) reports as having a loop more rounded anteriorly than is usual for the genus, and he states that Dall (1920: 324) questions the generic affinities of *E. trigona*. This might also prove to belong to *Notozyga*.

Etymology

From the Latin *gracilis* meaning slender, referring to the form of the loop.

Notozyga sp.

Fig. 13

Material

A single complete, dead specimen (SAM-A25467) from SM 131 at a depth of 780 m.

Description

Small biconvex shell, subpentagonal to elongately oval in outline; maximum width at about two-thirds valve length. Anterior commissure rectimarginate. Hinge line nearly straight, about seven-tenths as wide as valve. Interarea quite high, over one-third as long as valve; foramen large, triangular, flanked by narrow deltidial plates. Fairly broad, triangular palintropes between deltidial plates and beak ridges. Ornament consists of strong rounded costae, which become broader anteriorly and increase by branching. Posterolateral corners of brachial valve devoid of radial ornament. Concentric ornament of faint growth lines.

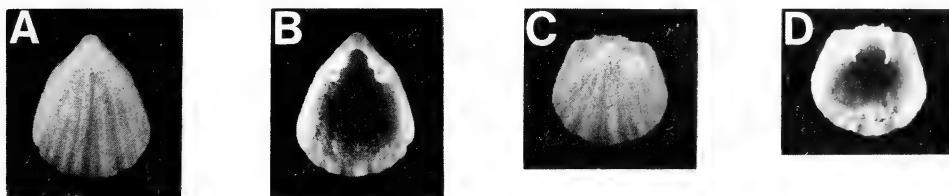


Fig. 13. *Notozyga* sp., SAM-A25467, SM 131. A-B. Ventral and interior views of pedicle valve. C-D. Dorsal and interior views of brachial valve. All $\times 8$.

Pedicle valve gently convex in lateral profile; quite strongly convex in anterior profile. Brachial valve evenly convex in both profiles.

Ventral interior with short, elevated pedicle collar and small teeth. Other details not seen. Dorsal interior with short, almost colinear socket ridges bounding small sockets. Stout crura, slightly flattened, projecting anteromedianly from valve wall in front of socket ridges. Remainder of loop not preserved.

Dimensions (mm)

	<i>Length</i>	<i>Width</i>
SAM-A25467	2,4	1,9

Discussion

This little specimen is placed in *Notozyga* on the basis of its well-defined ventral interarea, but it differs from *N. gracilis* sp. nov. in its more elongate outline and much stronger ribbing. However, more material with complete brachidia is required before another new species can be erected.

Subfamily Eucalathinae Muir-Wood, 1965

Genus *Eucalathis* Fischer & Oehlert, 1890*Eucalathis fasciculata* Cooper, 1973

Fig. 14

Eucalathis fasciculata Cooper, 1973b: 12, pl. 1 (figs 26–28).*Material*

Four complete specimens (SAM–A25468), live, from SM 60 at a depth of 800–810 m; one complete specimen (SAM–A25469), dead, from SM 103 at a depth of 680 m; seven complete, live specimens plus two brachial and two pedicle valves (SAM–A25470) from SM 246 at a depth of 1 640–1 660 m.

Description

Small, broadly triangular biconvex shells with narrow hinge and rounded anterior margin; posterolateral angles obtuse; maximum width, about twice hinge width, situated at around two-thirds valve length. Anterior commissure faintly uniplicate. Interarea very narrow; foramen wide, triangular; deltidial plates not always present but several specimens show development of symphytium. Pedicle relatively long, slender and frayed at end. Ornament consists of faint concentric growth lines and about 10 subangular primary costae, each of which gives rise to one or two costella to produce coarse fascicostellate ornament. Posterior portions of shell nearly smooth although faint traces of ribs may be seen.

Pedicle valve gently convex in lateral profile; anterior profile quite strongly convex in umbonal region but anterior of midvalve a weakly developed sulcus flattens profile. Brachial valve gently convex in lateral profile; inconspicuous fold originates near midvalve.

Pedicle valve interior with small teeth; pedicle collar developed; other details obscure. Brachial valve interior with stout socket ridges united posteriorly with wide, weakly developed cardinal process. Crura strong with blunt crural processes; loop short, triangular, with broad descending lamellae, which converge anteromedianly, and joined by narrow transverse band with small ventrally directed median fold.

Dimensions (mm)

	<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SAM–A25468	3,5	3,0	—
	3,1	2,8	1,5
A25469	2,8	2,3	1,2
A25470	2,7	2,4	1,4
	2,4	2,1	1,3

Loop dimensions (mm)

	<i>Length</i>	<i>Width</i>
SAM–A25468	1,5	0,7

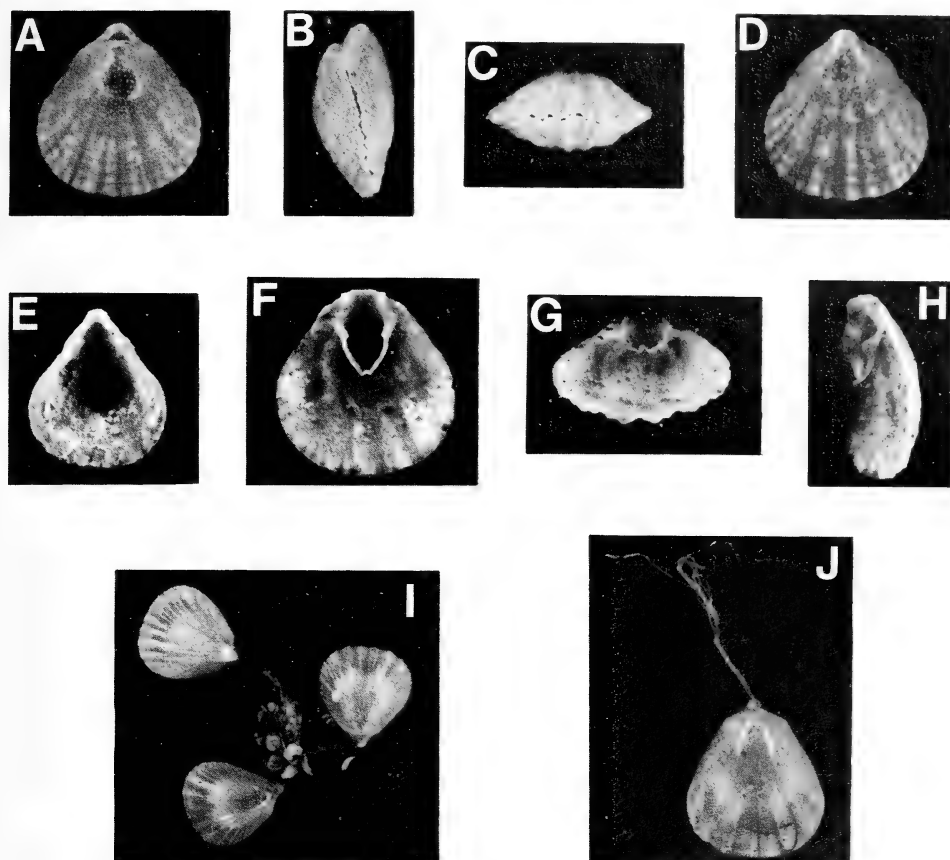


Fig. 14. *Eucalathis fasciculata* Cooper, 1973. A-D. SAM-A25470, SM 246: dorsal, lateral, anterior and ventral views of conjoined valves. E. SAM-A25469, SM 103: interior view of pedicle valve. F-H. SAM-A25470, SM 246: ventral, anterior and lateral views of brachial valve interior showing loop. I-J. SAM-A25468, SM 60. I. Group of three specimens with pedicles attached to foraminifera. J. Complete specimen showing long frayed pedicle.
A-H, J $\times 8$. I $\times 6$.

Discussions

These specimens can immediately be referred to *Eucalathis fasciculata* Cooper from south of Madagascar. It is distinguished from the other known species of the genus by its small size and distinctive ornament. This is the only species in which the posterior part of the shell is more or less smooth. The other Indian Ocean species, all from south of Madagascar, are *E. costellata* Cooper, *E. rotundata* Cooper, and an unnamed species recorded by Cooper (1981: 19). All of these forms have a strongly developed radial ornament.

Subfamily Agulhasiinae Muir-Wood, 1965

Genus *Agulhasia* King, 1871*Agulhasia davidsoni* King, 1871

Fig. 15

Agulhasia davidsoni King, 1871: 111, pl. 11 (figs 1–7). Thomson, 1927: 182, fig. 52. Helmcke, 1940: 242, fig. 7. Jackson, 1952: 9. Cooper, 1973b: 14, pl. 4 (figs 1–14); 1973c: 15, pl. 8 (figs 18–24).

Terebratulina (Agulhasia) davidsoni King: Davidson, 1886: 36, pl. 7 (figs 1–5).

Material

Nine complete specimens (SAM–A25471) from SM 131 at a depth of 780 m. All appear to have been dead and sediment-filled at time of collection. Some show signs of abrasion suggesting transportation from living site.

Description

Small biconvex shells with broadly triangular outline; maximum width near anterior margin. Anterior commissure gently uniplicate. Ventral beak greatly elongate, about one-third as long as shell, narrowly pointed; delthyrium bounded by pair of disjunct deltidial plates and almost closed by long, triangular, concave apical plate, which restricts foramen to a small opening at anterior end of beak. Radial ornament consists of rounded costae and costellae; most specimens had 6 (pedicle valve) or 7 (brachial valve) primary costae extending from umbo, secondary ribs arise mostly by intercalation between primaries from about 1 mm growth stage to give total of 11 or 12 ribs by 2 mm growth stage. Largest specimens with 18–22 ribs at anterior margin. Radial ornament absent from lateral margins of both valves. Concentric ornament of closely spaced growth lines.

Pedicle valve elongately triangular; lateral profile evenly convex; anterior profile with median flattening and development of broad shallow sulcus in later growth stages. Brachial valve elongately subpentagonal; lateral profile with maximum convexity near umbo; anterior profile arched along midline but true fold not developed.

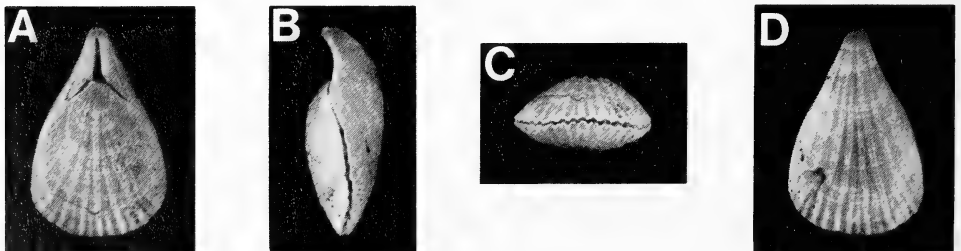


Fig. 15. *Agulhasia davidsoni* King, 1871, SAM–A25471, SM 131. A–D. Dorsal, lateral, anterior and ventral views of conjoined valves. All $\times 8$.

Details of internal characteristics of valves not available from present specimens, but see Cooper (1973b: 14).

Dimensions (mm)

	<i>Length</i>	<i>Width</i>
SAM-A25471	4,5	2,9
	4,0	2,6
	3,4	2,3
	2,3	1,5
	2,4	1,7
	1,6	1,0
	2,2	1,4
	2,9	1,9
	1,8	1,1

Discussion

Agulhasia davidsoni King is characterized by its small size, broadly triangular shape and especially by its elongated ventral beak. It is unlikely to be mistaken for any other species. It is known only from South African waters.

Suborder TEREBRATELLIDINA Muir-Wood, 1955

Superfamily TEREBRATELLACEA King, 1850

Family **Kraussinidae** Dall, 1870

Genus *Kraussina* Davidson, 1859

Kraussina rubra (Pallas, 1766)

Fig. 16

Anomia rubra Pallas, 1766: 182, pl. 14 (figs 2–11).

Terebratula capensis Küster (*non* Adams & Reeve), 1848: 32, pl. 3 (figs 15, 17).

Terebratula capensis Krauss (*non* Adams & Reeve), 1848b: 32, pl. 2 (fig. 10).

Terebratula (*Kraussia*) *rubra* (Pallas): Reeve, 1861: 9, fig. 37.

Kraussina rubra (Pallas): Davidson, 1887: 119, pl. 20 (figs 19–23). Jackson, 1952: 22, pl. 3 (figs 1–2). Cooper, 1973c: 23, fig. 5, pl. 9 (figs 10–22).

Material

A broken pedicle valve (SAM-A25472) from SM 129 at a depth of 850 m; a complete specimen and a pedicle valve (SAM-A25473) from SM 131 at a depth of 780 m; and a complete specimen (SAM-A25474) collected live from SM 185 at a depth of 90 m. Also included in this description are two specimens separated from coral material collected during earlier research expeditions: a complete

immature specimen (SAM-A25484) with coral SAM-H1366 dredged 28 December 1898 by S.S. *Pieter Faure* at station PF 796 (33°4'S 27°57'E) at a depth of 59 m; and a complete specimen (SAM-A25483) collected live at Somerset Strand, 23 October 1897, with coral SAM-H1406.

Description

Biconvex shells with width usually slightly less than length; outline variable but usually elongately oval. Hinge line nearly straight, about seven-tenths as wide as valve. Anterior commissure gently sulcate. Beak suberect, irregularly truncated with large incomplete submesothyriddid foramen bounded by small triangular deltidial plates. Narrow triangular palintropes between deltidial plates and beak ridges. Ornament consists of concentric growth lines and strong rounded costae, which increase by branching and intercalation; 18–22 ribs on pedicle valve at 5 mm growth stage.

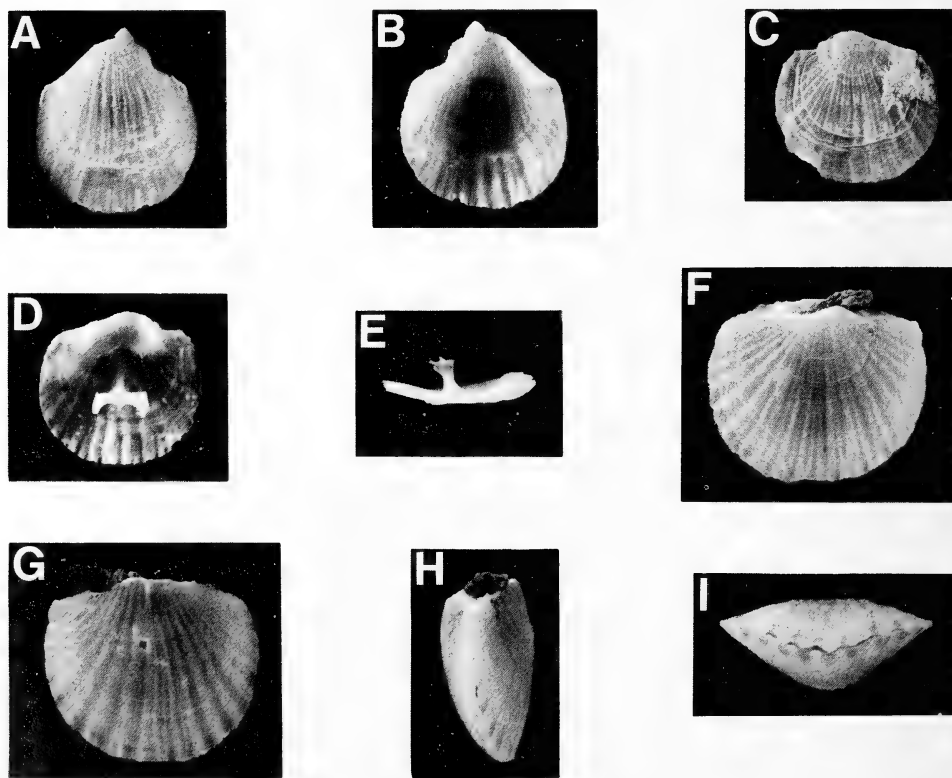


Fig. 16. *Kraussina rubra* (Pallas, 1766). A-E. SAM-A25483, Somerset Strand. A-B. Ventral and interior views of pedicle valve. C-D. Dorsal and interior views of brachial valve. E. Lateral view of brachidium. F-I. SAM-A25474, SM 185: dorsal, ventral, lateral and anterior views of conjoined valves with pedicle. A-E $\times 2$. F-I $\times 4$.

Pedicle valve gently convex in lateral profile but broadly carinate in anterior profile. Brachial valve gently convex in lateral profile, anterior profile with broad shallow sulcus extending from near umbo, separating gently convex flanks.

Pedicle valve interior with small teeth without dental plates; pedicle collar short, sessile but may be slightly excavate anteriorly. Other details obscure. Brachial valve interior with low, widely divergent socket ridges bounding narrow sockets. Cardinal process transversely elliptical, between posterior ends of socket ridges. Notothyrial platform consists of a pair of suboval thickenings between socket ridges and posterior end of median septum; in middle of each, rounded depressed attachment scars of pedicle muscles are situated. Low median septum extends from in front of notothyrial platform and supports at its distal end a pair of diverging lamellae, extending ventrally. Ventral end of each lamella drawn out into short anteriorly directed prong; some specimens also bear posterior prongs and some have short spine on top of each lamella. Valve floors of small specimens show radial rows of coarse tubercles but these are not seen in adult shells. Occasional small submarginal spines present in some specimens.

Dimensions (mm)

	<i>Length</i>	<i>Width</i>
SAM-A25472	7,2	c. 7
A25473	3,6	3,0
	4,1	3,2
A25474	5,7	7,3
A25483	12,2	10,9
A25484	1,7	1,3

Discussion

Kraussina is a fairly common genus in Cape coastal waters and is represented by the species *K. crassicostata* Jackson, *K. cognata* (Sowerby) and *K. rubra* (Pallas), which is perhaps the most common of all brachiopod species in this part of the world. *Kraussina crassicostata* can immediately be separated from the others by its smaller size, more convex valves and stronger, coarser ornament. *Kraussina cognata* is poorly known and more material is required for its relationship to *K. rubra* to be fully assessed. It is recorded from western Cape waters whereas *K. rubra*, while known from the western Cape coast, is more commonly found on the east coast. From previous descriptions, e.g. Jackson (1952: 24), it seems that the principal difference between *K. cognata* and *K. rubra* is one of colour; the former is reported to be pale yellow whereas the latter is noted for its red and white markings although the author has seen pure white shells in a sample of otherwise coloured specimens. Colour alone is a most unsatisfactory criterion on which to separate species.

Of the present specimens, the very small shells are white but one has reddish markings around its anterior margin and the specimen separated from coral SAM-H1406 is yellowish. This last specimen may prove to be *K. cognata* but for the present it is included with the others in *K. rubra*, which has such a variable

shape that growth ratios are virtually useless in separating species. The species are rather poorly defined and in need of revision so that the full range of morphological variation can be taken into account when distinguishing between them.

Genus *Megerlia* King, 1850

Megerlia acrura sp. nov.

Fig. 17

Diagnosis

Megerlia similar in most respects to *M. gigantea* (Deshayes) but without the development of crura.

Material

Holotype. SAM-A25475 in the South African Museum, Cape Town. From SM 239 (32°14,8'S 29°00,8'E) at a depth of 90 m, 25 June 1979.

Paratypes. SAM-A25476 in the South African Museum, Cape Town. From SM 239 (32°14,8'S 29°00,8'E) at a depth of 90 m, 25 June 1979. SAM-A25477 in the South African Museum, Cape Town. From SM 255 (31°37,8'S 29°40,8'E) at a depth of 125 m, 28 June 1979.

All the specimens were live at time of collection; that from SM 255 is a juvenile.

Description

Small subcircular to roundedly subrectangular shells with width slightly greater than length. Anterior commissure broadly and very gently sulcate. Beak broadly rounded; foramen hypothyriddid, bounded by small, narrow, raised deltidial plates. Interarea flat to gently curved.

Ornament on pedicle valve consists of concentric growth lines, faintly developed costellae, tubercles and small bristle-like spines; brachial valve ornament of faint ribs and growth lines but no spines or tubercles. Pedicle short and thick.

Pedicle valve strongly and evenly convex in lateral profile; anterior profile more arched medianly with flatter, sloping flanks. Brachial valve varying from almost flat to gently convex especially in umbonal region; anterior profile evenly convex.

Pedicle valve interior with short, slightly excavate pedicle collar and strong teeth. Large subcircular pedicle muscle scars situated on either side of median line about one-third valve length from posterior margin. Brachial valve interior with high thickened socket ridges bounding relatively narrow sockets; no cardinal process. Between socket ridges, thickened triangular platform passes anteriorly into low median ridge, which extends to about midvalve and supports at its anterior end a pair of anteroventrally directed plates, which form an open V-shape when viewed from anterior. At about two-thirds of their height, posterior margins of plates give rise to fine ribbon-like lamellae, which unite postero-medianly to form complete ring. From about one-third of their height, anterior

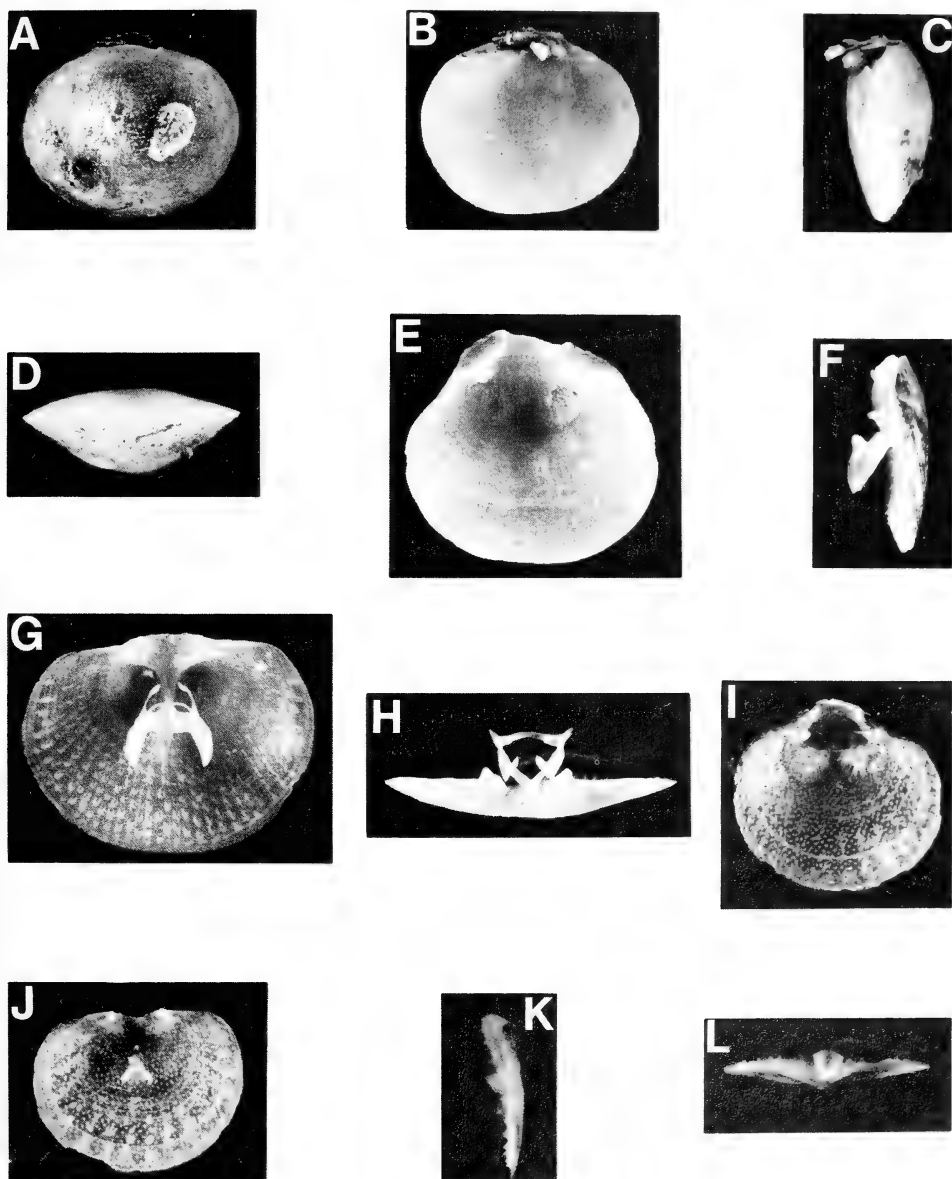


Fig. 17. *Megerlia acrura* sp. nov. A-D. SAM-A25475, holotype, SM 239: ventral, dorsal, lateral and anterior views of conjoined valves with pedicle. E-F. SAM-A25476, paratype, SM 239. E. Interior view of pedicle valve. F. Lateral view of brachidium. G-H. SAM-A25475, holotype, SM 239: ventral and posterior views of brachial valve interior showing brachidium. I-L. SAM-A25477, paratype (juvenile), SM 255. I. Interior view of pedicle valve. J-L. Ventral, lateral and posterior views of brachial valve interior showing precampagiform stage brachidium. A-F $\times 3$. G-H $\times 4$. I-L $\times 8$.

margins of plates give rise to another pair of ribbon-like lamellae, which extend and converge posteriorly but do not meet. In none of the specimens is there any sign of crural development. Diductor muscles attached to thickened notothyrial platform between socket ridges; adductors located on valve floor anterior to this, on either side of median ridge. Outside muscle field, valve floor covered in coarse, radially disposed tubercles, which increase in size towards valve margin.

Dimensions (mm)

		<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SAM-A25475	Holotype	9,9	10,9	—
SAM-A25476	Paratype	8,1	9,8	4,0
SAM-A25477	Paratype	3,2	3,4	1,1

Discussion

In most respects these specimens are very similar to *Megerlia gigantea* (Deshayes), including the strong re-entrant at the dorsal beak suggesting an amphithyridid foramen. The principal difference with this, and indeed other species in the genus, is that none of the specimens described here shows any sign of the development of crura. The juvenile specimen shows an early stage (pre-campagiform) in loop development with a small cone, open anteriorly, supported on a short pillar, similar to the situation described by Cooper (1981: 28) in specimens of similar size. However, this specimen shows no sign of incipient crus development as shown by Cooper's specimens. Cooper (1981, pl. 6 (figs 9, 16, 22)) also figures adult specimens of similar size to the large *Meiring Naude* specimens, in which the crura are fully developed and extend from in front of the socket ridges to join the rest of the brachidium. No such development is seen in the present specimens, which are thus distinguished by their lack of crura.

Etymology

The specific name refers to the lack of crura.

Genus *Megerlina* Deslongchamps, 1884

Megerlina pisum (Lamarck, 1819)

Fig. 18

Terebratula pisum Lamarck, 1819: 245.

Terebratula natalensis Krauss, 1844 (plates), pl. 2b (figs 4–7); 1848a (text): 36.

Material

One dead specimen (SAM-A25478) from SM 163 at a depth of 90 m; one live specimen (SAM-A25479) from SM 179 at a depth of 80 m; one dead specimen (SAM-A25480) from SM 180 at a depth of 80 m; and seven live and four dead specimens plus a few fragments (SAM-A25481) from SM 185 at a depth of 90 m. Also included in this description are two specimens separated from coral material collected during an earlier research expedition: a complete

live specimen (SAM-A25485) with coral SAM-H1365 dredged 29 August 1901 by S.S. *Pieter Faure* at station PF 13601, 8 km W by N of Great Fish Point Lighthouse at a depth of c. 41 m; a complete live specimen (SAM-A25486) with coral SAM-H1383 dredged 25 September 1901 by S.S. *Pieter Faure* at station PF 13959, 4,8 km N by E $\frac{3}{4}$ E of Bird Island Lighthouse at a depth of c. 66 m.

Description

Subpentagonal to subquadrate shells with length and width about equal; maximum width about midvalve. Pedicle valve slightly deeper than brachial valve. Anterior commissure sulcate. Hinge line nearly straight, about three-fifths as wide as valve. Beak suberect with large incomplete submesothyridid foramen bounded by small triangular deltidial plates. Narrow triangular palintropes between deltidial plates and beak ridges. Ornamentation of rounded costellae, which increase by branching and intercalation; 24–33, most commonly 27, ribs at 5 mm growth stage on brachial valve.

Pedicle valve gently convex in lateral profile; anterior profile broadly carinate. Median fold narrow, extending from near umbo becoming broader and more prominent anteriorly; lateral slopes flat to very gently convex. Brachial valve over four-fifths as long as pedicle valve, gently convex in both profiles. Narrow shallow median sulcus extends from close to umbo, becoming broader and deeper anteriorly.

Pedicle valve interior with small teeth; pedicle collar very short, slightly excavate anteriorly. Radially disposed tubercles cover anterior part of valve floor; occasional spine present just inside anterior margin. Brachial valve interior with strong socket ridges and fulcral plates bounding narrow deep sockets. Notothyrial platform defined by buttresses joining anterior ends of socket ridges to medium septum; cardinal process elliptical, weakly developed. Medium septum extends from in front of cardinal process to just anterior of midvalve. At its anterior end it supports a brachidium consisting of a pair of anteroventrally directed diverging lamellae. Each lamella bears, at its distal end, a small prong that projects posteromedianly, and midway down the outer surface of each lamella is an accessory ledge (or process). Valve floor covered by radial rows of coarse tubercles. Muscle scars lightly impressed on notothyrial platform and valve floor immediately anterior to platform.

Dimensions (mm)

	<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SAM-A25478	8,3	8,3	3,5
A25479	6,9	6,4	2,7
A25480	4,7	4,4	1,8
A25481	6,4	6,3	—
	5,2	4,9	1,9
A25485	6,1	6,2	2,5
A25486	4,5	4,3	1,6

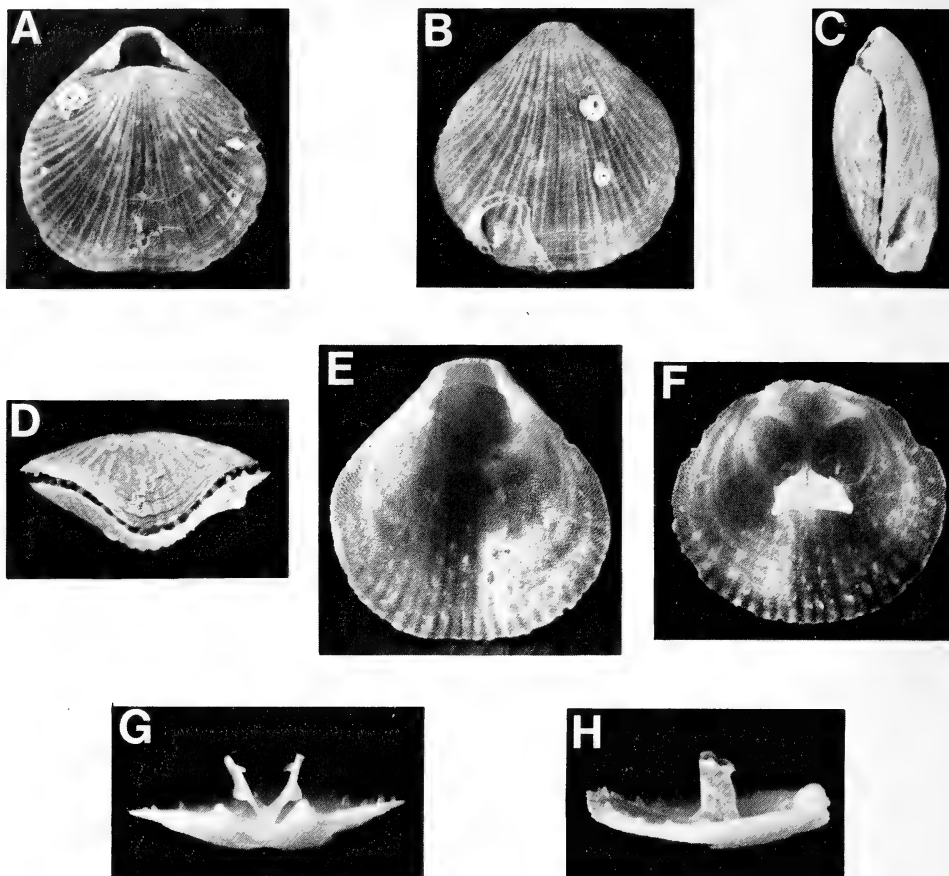


Fig. 18. *Megerlia pisum* (Lamarck, 1819). A–D. SAM–A25478, SM 163: dorsal, ventral, lateral and anterior views of conjoined valves with serpulid worm tubes. E–H. SAM–A25481, SM 185. E. Interior view of pedicle valve. F–H. Ventral, posterior and lateral views of brachial valve interior showing brachidium. A–D $\times 4$. E–H $\times 6$.

Discussion

No less than four species of *Megerlina* have been recorded from the same area off the eastern Cape coast from which the present specimens were recovered. Previous descriptions of these species, *M. pisum* (Lamarck), *M. natalensis* (Krauss), *M. capensis* (Adams & Reeve) and *M. striata* Jackson, have been based on very few specimens and it is unlikely that the full extent of the variation within the genus has been properly assessed, with the result that the relationships between these four species are unknown.

The earlier descriptions distinguish between species on characters such as colour, strength of ribbing, depth of sulcus and size and shape of the punctae. The *Meiring Naude* specimens are all whitish in colour but pink or red around the

margins. In this they are similar to the first three species named above. Their strength of ribbing suggests affinities with both *M. striata* and *M. capensis* but no figures of rib numbers are available for comparison. *Megerlina pisum* and *M. natalensis* have less pronounced ribbing and may be smooth umbonally.

The depth of sulcus depends on the size of the shell, so comparisons should only be made between specimens of approximately equal length; again examples of other species are needed for comparison. In shape and density, the punctae of the *Meiring Naude* specimens show closest similarity with the figures given by Jackson (1952: 31) for *M. pisum* although the range overlaps with the ranges for other species.

Wright (1972: 5) showed the range of variation that was possible within a single species depending on its habitat especially when strength of ribbing and colour were considered. It may be that the species of *Megerlina* recorded from off the eastern Cape are simply variants of one species, *M. pisum*, so until such time as re-assessment of these species is carried out, it is felt that the *Meiring Naude* specimens are best identified as *M. pisum*.

Family **Phaneroporidae** Zezina, 1981

Genus *Leptothyrella* Muir-Wood, 1965

Leptothyrella cf. *ignota* (Muir-Wood, 1959)

Fig. 19

Leptothyris ignota Muir-Wood, 1959: 308, pl. 4 (fig. 9), pl. 5 (figs 12–14).

Material

A single slightly damaged specimen (SAM-A25482) from SM 129 at a depth of 850 m. The specimen was dead at time of collection and shell was partially filled with sediment.

Description

Small shell with elongately oval pedicle valve and almost circular brachial valve; both valves gently and evenly convex, anterior commissure rectimarginate. Ventral beak quite narrow, nearly straight; foramen hypothyridid; delthyrium open with no, or extremely narrow, deltidial plates. Shell surface smooth except for concentric growth lines. Punctae coarse.

Pedicle valve interior with strong teeth without dental plates; pedicle collar broad, sessile, extending almost full length of delthyrium; broad, low, median ridge extends to about two-thirds valve length. Brachial valve interior with strong high socket ridges bounding fairly deep sockets; no cardinal process. Rounded, narrow crura extend from anterior ends of socket ridges towards median septum, anterior ends becoming flatter. High, pillar-like median septum originates in front of notothyrial cavity and extends to about midvalve. No ring or hood present.

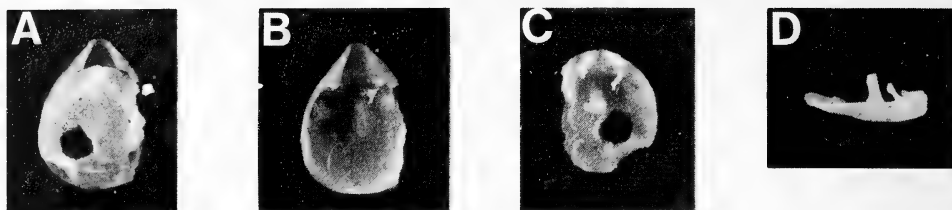


Fig. 19. *Leptothyrella* cf. *ignota* (Muir-Wood, 1959), SAM-A25482, SM 129. A. Dorsal view of conjoined valves. B. Interior view of pedicle valve. C-D. Ventral and lateral views of brachial valve interior showing brachidium. All $\times 8$.

Dimensions (mm)

	Length	Width
SAM-A25482	2,5	1,8

Discussion

The inwardly directed crura, high pillar-like septum, wide foramen with incipiently developed deltidial plates of this little specimen all point to an early growth stage of a terebratulacean. However, the poorly known *Leptothyrella ignota* (Muir-Wood) from off Zanzibar and the Gulf of Aden is remarkably similar, although Muir-Wood's specimens, which the author has examined, are larger at 5 mm length. Both forms are coarsely punctate and have the same overall shell outline with gently convex valves and rectimarginate anterior commissure. Both have an open delthyrium flanked by extremely narrow deltidial plates and floored by a pedicle collar that extends almost the full length of the delthyrium. The brachial valve of *L. ignota* has a high, plate-like median septum, which does not continue posteriorly into the notothyrial cavity; the crura are slender and curved; the cardinal process is minute.

Any differences between *L. ignota* and the shell described here can be accounted for by the larger size and presumably more adult nature of *L. ignota*, by which stage the tiny cardinal process has developed as have the points of attachment of the descending branches to the median septum. Otherwise both forms are so similar that they must be regarded as being very closely related.

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Family **Nuculanidae**

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

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Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region. King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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NORTON HILLER

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LATE TERTIARY AND EARLY
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OF THE HONDEKLIP AREA,
CAPE PROVINCE, SOUTH AFRICA

By
BRIAN KENSLEY
&
JOHN PETHER

Cape Town Kaapstad

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LATE TERTIARY AND EARLY QUATERNARY FOSSIL MOLLUSCA OF THE HONDEKLIP AREA, CAPE PROVINCE, SOUTH AFRICA

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(With 42 figures and 1 table)

[MS accepted 10 February 1986]

ABSTRACT

A brief review of the Quaternary mollusc research of the west coast of South Africa is provided. Molluscan fossils were obtained from two coastal regressive sedimentary complexes. The older complex records a regression from c. +50 m, and is called the 50 m Complex. Stratigraphic context in terms of global sea-level curves and the presence of *Equus* in this complex suggests a Late Pliocene age. The subsequent complex records a regression from c. +30 m, is called the 30 m Complex, and is considered Early Pleistocene in age.

The following 21 species and one subspecies are described as new: *Patella hendeyi*, *Patella hoffmani*, *Clanculus lutosus*, *Gibbula zonata patula*, *Bolma anoropha*, *Crepidula deprima*, *Argobuccinum casus*, *Epitonium lycocephalum*, *Thais arenae*, *Ocenebra petrocyon*, *Trophon carringtoni*, *Burnupena rogersi*, *Burnupena aestus*, *Fasciolaria dinglei*, *Melapium hawthornei*, *Pseudoliva lutulenta*, *Drillia tempestae*, *Terebra canisaxi*, *Glycymeris fulleri*, *Isognomon gariesensis*, *Cardita unica*, *Dosinia sicarisinus*. A number of previously described mollusc species are discussed or redescribed. The faunal composition and biogeography of the Hondeklip assemblage are discussed, and the assemblage is compared with other west-coast fossil assemblages. Temperature tolerances of some extant forms present indicate that a warmer water regime relative to modern conditions existed along the Namaqualand coast during the Late Pliocene and Early Pleistocene. A temperature contrast across the Plio-Pleistocene boundary is not clear-cut due to the faunal similarity of the 50 m and the 30 m Complexes. Significantly, about 50 per cent of the fauna is extinct. Decreased diversity and the appearance of *Choromytilus meridionalis* in the 30 m Complex may indicate cooling in the Early Pleistocene. Subsequently, the restriction of warmer waters to the north led to the establishment of the modern west-coast fauna. Lack of a broader regional database precludes more precise conclusions at this stage.

CONTENTS

	PAGE
Introduction	142
Geological setting	142
The Hondeklip and Avontuur A deposits	144
The Koningnaas and Swartlintjiesrivier localities	148
Systematic descriptions	149
Discussion	210
Faunal composition	210
Zoogeographic affinities	217
Faunal comparisons	219
Concluding remarks	221
Acknowledgements	223
References	223

INTRODUCTION

The fossil mollusc occurrences on the west coast of South Africa have received scattered attention during the past 50 years, with reports becoming more numerous in the last decade. Haughton (1932) presented an overview of the west-coast deposits and described several of the fossil molluscs. Barnard (1962) listed all the known Late Tertiary and Pleistocene molluscs from South Africa. New species and records for the west coast have since been added by Carrington & Kensley (1969), Kilburn & Tankard (1975), and Kensley (1972, 1977).

Diamond-mining activities on the Namaqualand coast have exposed coastal marine deposits in several areas. Fossil molluscs from three localities, Koingnaas, Swartlintjesrivier, and Strandfontein, were the subject of the paper by Carrington & Kensley (1969). Material recorded in the present paper also comes from Koingnaas, plus two additional properties, Avontuur A, and Hondeklip (Fig. 1A, B). Exposures of several fossil-bearing beds were bulk-sampled, while selective sampling was carried out when appropriate.

The bulk of the material recorded in the accompanying list (Table 1) is housed in the South African Museum, as are holotypes and paratypes, which bear SAM-PQ catalogue numbers. Where possible, paratypic material has also been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. and bears USNM catalogue numbers.

GEOLOGICAL SETTING

This paper is a sequel to that of Carrington & Kensley (1969) in which several new species obtained from similar deposits were described and a summarized general account of the Cenozoic coastal Namaqualand stratigraphy was presented. Important observations recorded in that work were the recognition of two distinct littoral marine complexes, the 45–50 m and the 17–21 m transgression complexes, and their zone fossils *Donax haughtoni* Carrington & Kensley, and *Donax rogersi* Haughton, respectively. The complex names indicate perceived transgressive altimetric maxima. The older 45–50 m complex was considered typified by fine, green quartzose sands and the associated thin-shelled *D. haughtoni*, while the younger 17–21 m complex was characterized by brown-stained, coarse, quartzo-feldspathic sands, high-energy bedforms, and the robust *D. rogersi*. An evolutionary relationship was inferred between the two *Donax* species, and linked to the changed environment implicit in the contrasted lithologies of the two complexes. Additionally, species obtained from the 45–50 m complex suggested a fauna of warm-water affinity.

Subsequent fieldwork on the properties of Hondeklip and Avontuur A has furnished more information on the depositional environments, ages, and sea-level history of the 45–50 m and 17–21 m complexes. This work will be presented in detail in another article (Pether in prep.); thus only a condensed account is given here. Modifications of the succession presented by Carrington & Kensley (1969) are shown in the following summarized stratigraphy.

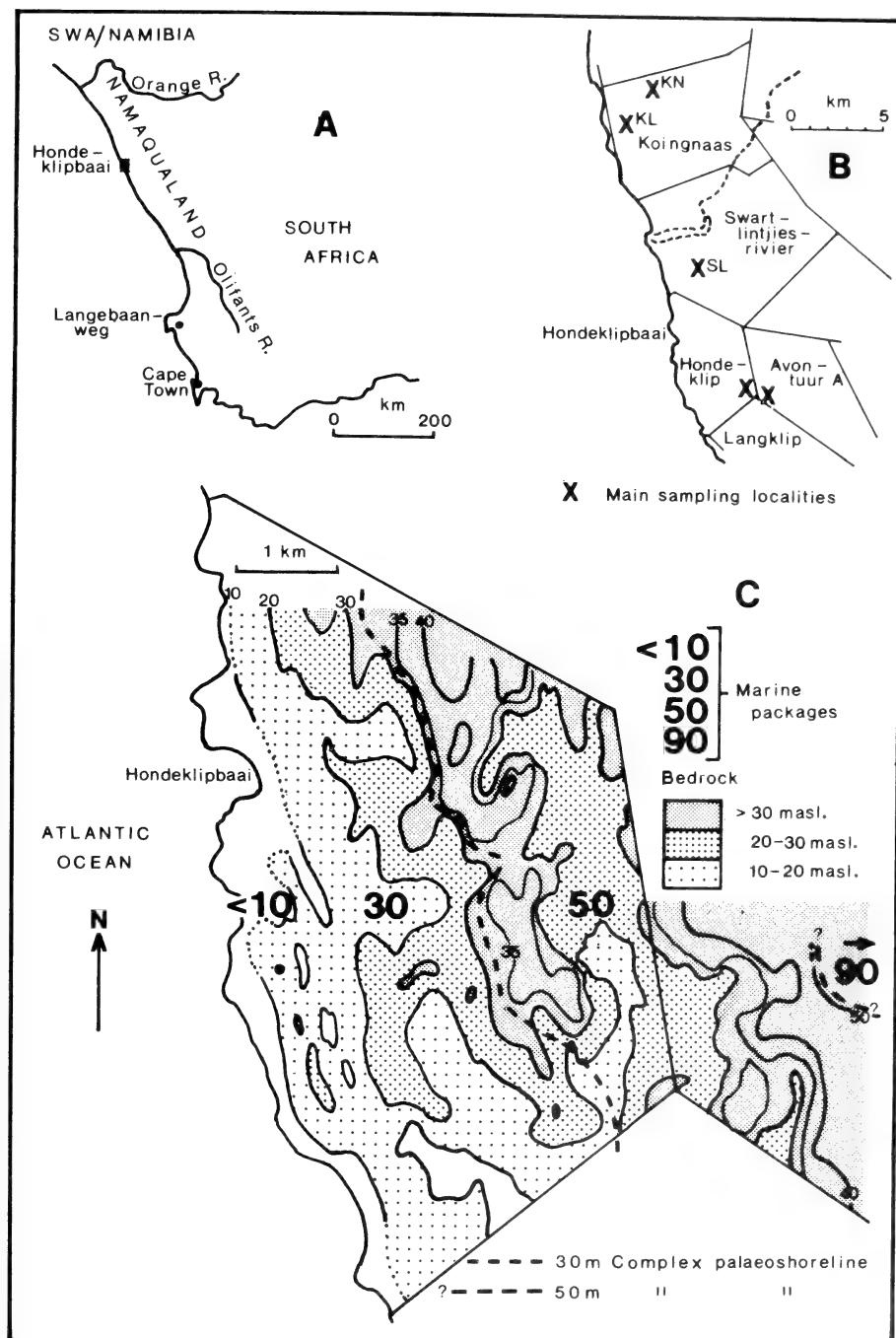


Fig. 1. A. Locality map. B. Hondeklip and surrounding properties with main sampling areas indicated. C. Bedrock contour map of Hondeklip and a portion of Avontuur A in metres above sea-level (masl). Large numerals (90, 50, 30) indicate the overlying deposits of the marine complexes; < 10 refers to the low-elevation, Mid-Pleistocene to Holocene raised beaches. Palaeoshorelines at transgressive maxima of the 30 m and 50 m Complexes are shown.

<i>Succession</i>	<i>Age</i>
*2 metre Beach	Holocene
*5 metre Beach	Late Pleistocene
8 metre Beach	Middle Pleistocene
30 metre Complex	Early Pleistocene
Regressive complex (incl. 29–34 m Beach and 17–21 m Complex)	
50 metre Complex	Late Pliocene
Regressive complex (= 45–50 m Complex)	
90 metre Complex	Early Pliocene
Regressive complex? (= 75–90 m Complex)	
(Includes lower shoreface to offshore deposits preserved in bedrock depressions underlying the 50 m Complex at lower elevations.)	
Kaolinized fluvial deposits	Latest Oligocene to Early Miocene
Bedrock	Archaean

THE HONDEKLIP AND AVONTUUR A DEPOSITS

Bedrock

The bedrock consists of Archaean quartzo-feldspathic gneiss, and bedrock topography (Fig. 1C) has profoundly influenced the local character of the overlying deposits. A major feature in the study area is a broad, coast-parallel, channel-like structure in the bedrock, which has its western flank defined by a bedrock ridge. Emergence of the bedrock ridge during regression resulted in a barrier along the seaward flank of the channel, protecting the channel area from open-coast conditions.

Kaolinized fluvial deposits

This, the oldest sedimentary entity encountered, is locally preserved in a bedrock depression. It is the remains of a fluvial arkosic infill deposited in the bedrock channel. The underlying bedrock and this fluvial infill are kaolinized and associated with it are silcrete slabs and boulders that are indurated portions of the fluvial deposits that have been exhumed by extensive erosion.

The bedrock is considered to have been incised during the major Oligocene regression that has been identified in the offshore record (Siesser & Dingle 1981). Subsequently, infilling Late Oligocene to Earliest Miocene fluvial deposits were kaolinized during the Early Miocene under tropical conditions; within the weathering profile titanium-rich silcrete developed. Sea-level fluctuations and concomitant marine and fluvial erosion during Middle Miocene to Late Pliocene times exhumed and modified the bedrock channel. No Miocene marine deposits are preserved.

* After Hendey & Volman (1986)

The 90 m Complex deposits

This high elevation complex, the 75–90 m Complex of Carrington & Kensley (1969), is present between 50–90 m above sea-level (masl), but no exposures at these elevations exist in the study area. However, underlying the younger 50 m Complex in a local bedrock depression, is a remnant deposit that may have been deposited, wholly or in part, during the same sea-level cycle. This is a partly indurated, mouldic, coquinoid, muddy conglomerate, which exhibits extensive (though not laterally continuous), authigenic phosphorite (microphosphorite) deposition. A ubiquitous, similar, phosphorite gravel content in overlying 50 m Complex gravels indicates the erosion of this previously more extensive lithology.

Fragmentary, worn, phosphate-mineralized, marine and terrestrial vertebrate fossils are associated with this bed. These have a Mio-Pliocene aspect (Q. B. Hendey pers. comm.). The mouldic coquinoid fauna has both intertidal and offshore aspects. The bed is considered to have been storm-deposited in a lower shoreface to offshore environment during regression, in an embayed situation. Extensive microphosphorite precipitation driven by upwelling took place during calmer periods. This bed has previously been referred to as 'lower E stage' (e.g. Tankard 1975b, 1975c).

The 50 m Complex deposits

This complex is present mainly to the east of the bedrock ridge (Fig. 1C). Exposures in open-coast situations reveal a regressive vertical facies sequence of lower-shoreface, upper-shoreface, foreshore, and aeolian environments. The basal gravel is seen to be a transgressive veneer, which has been redeposited and supplemented during regression in a lower-shoreface context. The bedrock ridge promoted the development of back-barrier environments in its landward lee during regressive emergence.

Evidence of a minor transgressive sea-level fluctuation is preserved in this complex and consists of a laterally persistent surface produced in back-barrier deposits, an anomalously thick foreshore deposit, a vertical aspect to normally lateral open-coast barrier facies deposition, and a tidal inlet-dominated barrier overlying back-barrier deposits.

The 30 m Complex deposits

The 50 m Complex was eroded by a subsequent transgression and overlying the transgressive disconformity is the 30 m Complex. This is a seaward-thickening wedge, which, beneath foreshore deposits extending from the transgressive maximum near +30 m, progressively incorporates upper-shoreface, and then lower-shoreface deposits. This complex is preserved mainly to the west (seaward) of the bedrock ridge (Fig. 1C). Sea-level altitude relative to bedrock topography suggests that generally during 30 m Complex times the effect of bedrock topography was not as marked as during the previous sea-level cycle. In the study

area there is no evidence of back-barrier environments during 30 m Complex times.

The 30 m Complex subsumes the 17–21 m Complex and the 29–34 m Beach of Carrington & Kensley (1969). No evidence of a stillstand at c. 20 masl is present in Hondeklip exposures. Instead, 30 m Complex lower-shoreface gravels extend seawards from that elevation. However, the possibility that stillstands occurred subsequently during the regression cannot be dismissed at this stage. The complex is present almost up to the modern coastline, where it is overlapped by younger palaeoshorelines at elevations of less than 10 masl.

Age of the marine complexes

Onshore and offshore evidence of Tertiary sea-levels around southern Africa has been synthesized in a curve by Siesser & Dingle (1981) (Fig. 2A); this curve exhibits a general correspondence with the trends of global sea-level produced by Vail & Hardenbol (1979). Sea-level history and age inferred for the deposits at Langebaanweg (Fig. 2B) is consistent with the global sea-level record (Hendey 1981a, 1981b) and, pointing out the feasibility of altimetric correlation along the southern-African west coast, Hendey proposed a preliminary correlation scheme between Langebaanweg and west-coast localities involving the high-elevation (> 10 masl) deposits.

The correlation scheme was related to the sea-level curve of Vail & Hardenbol (1979). Beard *et al.* (1982) provided greater resolution for the Quaternary portion of the 'Vail curve' (sea-level cycles Q1 to Q8 (Fig. 2C)). Although methodological aspects and the chronology of the curve are controversial, it is accepted here as presented and considered to be of provisional utility. For example, Vail & Hardenbol (1979) and Beard *et al.* (1982) placed the Plio-Pleistocene boundary at 2,8 Ma; in contrast, in terms of the most recent ICS decision (Aguirre & Pasini 1985), the boundary at the Vrica section is ~1,64 Ma. Regardless of this controversy, it is the sea-level curves, as gross indicators, that are deemed relevant, and interestingly they do show a general correspondence with our present (though scant) knowledge of west-coast deposits. In this paper the Plio-Pleistocene boundary is taken at ~1,6 Ma; thus sea-level cycle Q1 (Fig. 2C) is considered Late Pliocene.

An important feature of Hendey's (1981a, 1981b) correlation scheme was the correlation of the 90 m Complex in Namaqualand with the Early Pliocene Varswater Formation at Langebaanweg; the latter, in turn, related to the transgressive sea-level period TP1 of Vail & Hardenbol (1979) (Fig. 2B). An Early Pliocene age for the 90 m Complex is consistent with observations at Hondeklip. The likelihood of the complex being a regressive package in Namaqualand suggests correlation with sea-level cycle TP2.

The presence of a species of *Equus* in the 50 m Complex suggests that it cannot be older than the 1,9 Ma mammalian dispersal event in Africa (Lindsay *et al.* 1980). Similar to the age inferred by Hendey (1981a) for the Baards Quarry Fluvatile Deposits in the south-western Cape which contain *Equus*, the 50 m

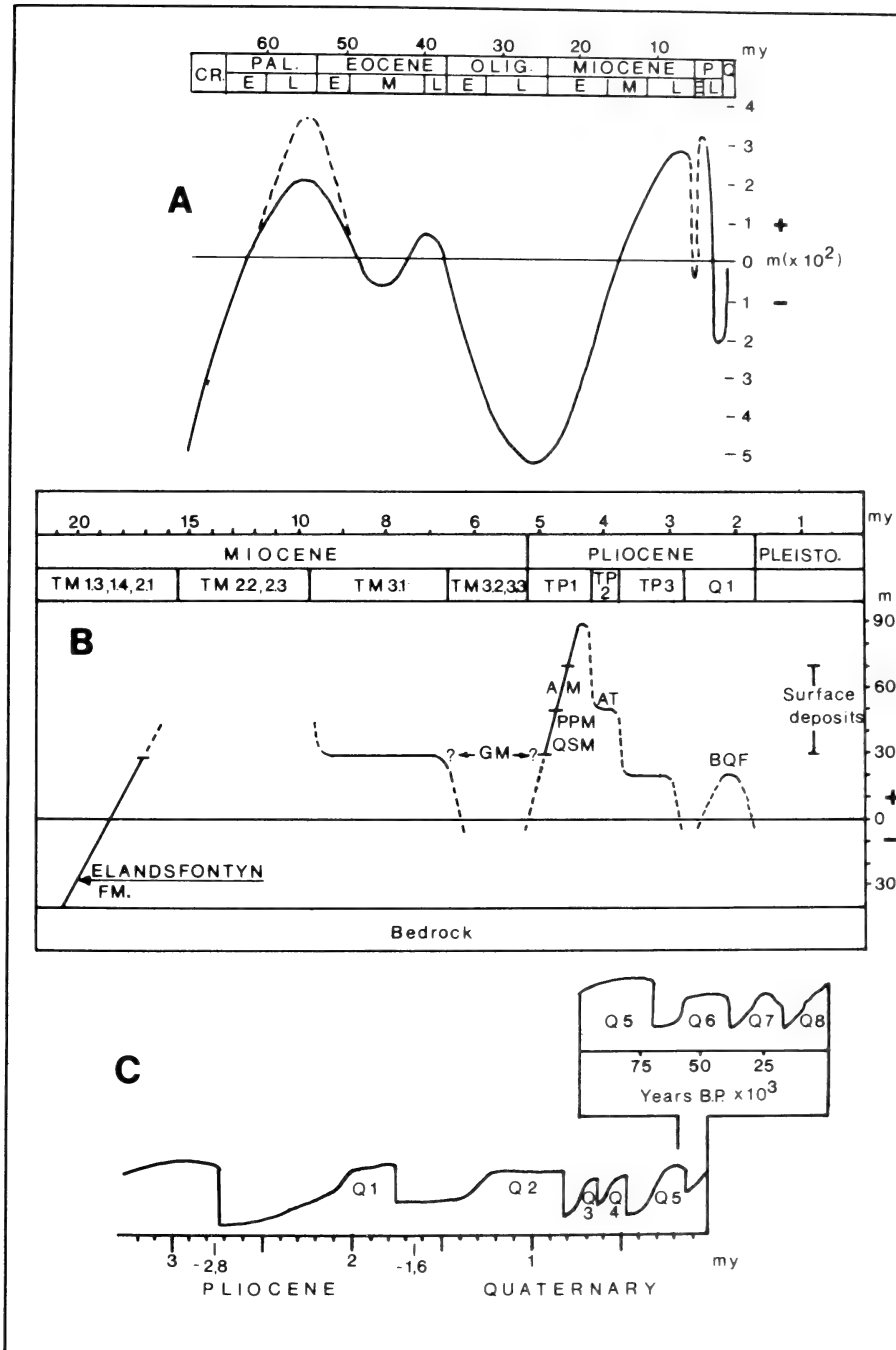


Fig. 2. A. Gross Tertiary sea-level trends after Siesser & Dingle (1981). B. Langebaanweg deposits (south-western Cape) related to global sea-level trends of Vail & Hardenbol (1979) (after Hendey 1981b). GM = Gravel Member, QSM = Quartzose Sand Member, PPM = Pelletal Phosphorite Member, AM = Anyskop Marine Deposits—all of the Varswater Formation. AT = Anyskop terrestrial deposits, BQF = Baard's Quarry fluvial deposits. C. Gross Quaternary sea-levels of Beard *et al.* (1982).

Complex is considered Late Pliocene in age and is correlated with the regressive portion of sea-level cycle Q1 of Vail & Hardenbol (1979) and Beard *et al.* (1982).

The 30 m Complex must reflect a subsequent high sea-level, and it is thus correlated with cycle Q2 in the Early Pleistocene. A Late Pliocene and Early Pleistocene age for the 50 m and 30 m Complexes, respectively, is probably consistent with the warmer-water faunal elements present, relative to the colder-water assemblages of the younger, low-elevation complexes and of the modern coast.

The age of these low-elevation (< 10 masl) palaeo-shorelines has recently been assessed (Hendey & Volman 1986). Fossil evidence associated with the 8 m Beach at Saldanha suggests a late Early Pleistocene age to Hendey & Cooke (1985) and it was correlated with sea-level cycle Q2. Since this report prefers to relate the 30 m Complex to cycle Q2, the 8 m Beach is here considered to reflect cycle Q3. This younger (Middle Pleistocene) age is inconsistent with the age constraints inferred from the fossil evidence at Saldanha, an issue yet to be resolved. The 5 m and 2 m shorelines are considered to be Late Pleistocene (Eemian) and Holocene respectively (Hendey & Volman 1986). Flemming (1977) has submitted evidence that the Flandrian transgression reached 3 masl and profoundly influenced the development of the Langebaan lagoon. Recently a radiocarbon date of 3800 BP has been obtained at 2,5 masl at Verlorelevlei (J. Parkington pers. comm.).

THE KOINGNAAS AND SWARTLINTJIESRIVIER LOCALITIES

Some basal exposures of the deposits on De Beers properties neighbouring Hondeklip (Fig. 1B) were examined and seen to contain molluscs not well represented at Hondeklip. In the case of the 50 m Complex outcrops (Koingnaas KN and Swartlintjies SL), this is due to the occurrence of thicker, muddy, distal lower shoreface deposits in bedrock depressions at these localities. At Hondeklip the deposits of this environment are thinner and more cryptic, due to the embayed palaeocoastal geomorphology formed by the bedrock topography, in contrast to the more open-coast, palaeocoastal situation considered applicable to the De Beers properties. This facies overlies bedrock or local 90 m Complex remnants, and is overlain by gravelly, proximal lower shoreface deposits of the 50 m Complex. It is characterized by a molluscan fauna with both intertidal and sublittoral components, and in these respects the similarity with the 90 m Complex remnants is noteworthy.

An outcrop of the 30 m Complex on Koingnaas also yielded species not encountered at Hondeklip (Koingnaas KL). At this exposure a massive sand, containing thin gravel beds and a mud lens ~20 cm thick, overlies bedrock at 10 masl. It attains its greatest thickness (~2 m) in a local bedrock depression. This unit is overlain by the 30 m Complex upper shoreface facies. It is thus interpreted as 30 m Complex proximal lower shoreface deposits. The open-coast forms *Isognomon* sp., *Macra* sp., and *Turritella carinifera* dominate the assemblage.

SYSTEMATIC DESCRIPTIONS

In the following section, in addition to the previously undescribed material, discussion is given to some previously recorded taxa, where relevant.

As is frequently the case in fossil molluscan systematics, generic allocation cannot always be done with certainty, due to the lack of essential diagnostic information (e.g. radular and opercular structure). This uncertainty in generic placement was constantly in the forefront of the authors' thoughts when writing descriptions; nevertheless it was decided not to indicate this uncertainty with quotation marks or any other such device.

Unless otherwise stated, all material mentioned in this work was collected by the authors.

Class GASTROPODA

Family **Haliotidae***Haliotis saldanhae* Kensley, 1972

Haliotis saldanhae Kensley, 1972: 176, fig. 2.

Material

SAM-PQ-AV229, several fragments, Avontuur A, Trench 3.

SAM-PQ-KN370, numerous fragments, including seven triangular fragments, each the upper columella portion of an individual shell, Koingnaas KN-1.

Previous records

Langebaanweg, Pliocene.

Remarks

Several large abalone specimens have been seen in situ at Avontuur, but the shell material is usually so fragile and friable as to make recovery almost impossible. Several fragments of shell, however, have been recovered, bearing the distinctive rounded spiral ridges and broadly rounded oblique axial ridges characteristic of *H. saldanhae*.

A single specimen (SAM-PQ-AV506), c. 60 × 140 mm, was recovered, which retains its overall shape and proportions. Unfortunately none of the exterior shell structure remains, making positive identification impossible. The size of this specimen places it well beyond the maximum for *H. spadicea* Donovan, 1808, but within the size range of living *H. midae* Linnaeus, 1758, of the west coast.

Family **Fissurellidae***Amblychilepas scutellum* (Gmelin, 1791)

Amblychilepas scutella: Barnard, 1962: 191; 1963: 286, figs 21b, 22d-f.

Amblychilepas scutellum: Kilburn & Rippey, 1982: 35, pl. 2 (fig. 11), pl. 6 (fig. 1a, b).

Material

SAM-PQ-HB319, 4 specimens; TL 22,5 mm, 23,3 mm, 29,0 mm, 1 damaged, Hondeklip Zone 12. SAM-PQ-HB74, 2 specimens, Hondeklip, 50 m Complex.

Previous records

Living: Angola to Natal.

Fossil: Saldanha, Little Brak River, Sedgefield, Durban, Inhambane.

Remarks

The living subspecies, *A. s. scutellum* of the west coast, is characterized by the possession of 'moderately to extremely raised ends' (Kilburn & Rippey 1982: 35). The present material consists of six specimens not at all saddle-shaped, i.e. sitting flat on a horizontal surface, and one specimen with very slightly raised ends.

Fissurellidea aperta (Sowerby, 1825)

Pupillaea aperta Sowerby, Barnard, 1962: 191.

Fissurellidea aperta (Sowerby) Barnard, 1963: 288, fig. 21e. Kensley, 1973: 32, fig. 46. Kilburn & Rippey, 1982: 36, pl. 3 (fig. 3), pl. 6 (fig. 13).

Material

SAM-PQ-KN507, 1 specimen, 22,8 × 12,8 mm, 4 fragments, Koingnaas KN-1.

Previous records

Living: Namibia to Transkei, shallow infratidal.

Fossil: Pleistocene, Algoa Bay.

Tugali barnardi (Tomlin, 1932)

Tugalia barnardi: Barnard, 1963: 300, figs 21d, 22a-c.

Material

SAM-PQ-KN392, 2 specimens, 4,0 × 2,8 mm, 8,1 × 4,6 mm, Koingnaas KN-1.

Previous records

Living: off Cape Point, 360 m; False Bay, 18 m; St. Francis Bay, 12 m.

Dead: Cape Point to Cape Morgan, intertidal to 360 m.

Remarks

The fossil specimens have been compared with material in the South African Museum, and agree very closely with specimens from St. Francis Bay (SAM-A9299). The external ridge sculpture is as figured by Barnard (1963: 291, fig. 22b).

Family *Patellidae**Patella hendeyi* sp. nov.

Figs 3, 4

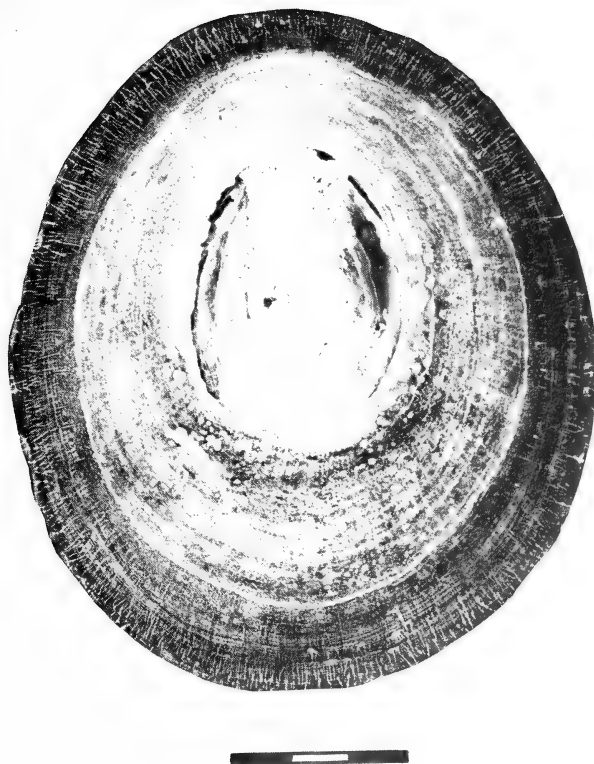
Patella sp. ('large') Haughton, 1932: 30.*Material**Holotype*. SAM-PQ-AV454, 126 × 107 mm, Avontuur A, 50 m Complex.*Paratypes*. SAM-PQ-AV455-457, 7 specimens, 68 × 57 mm, 74 × 61 mm, 90 × 76 mm, 94 × 77 mm, ? × 109 mm, 142 × 133 mm, 146 × 137 mm, Avontuur A, 50 m Complex. SAM-PQ-HB458, 148 × 130 mm, Hondeklip Z4A, 50 m Complex (with attached barnacle shells). USNM 400979, 2 specimens, 122 × 112 mm, 138 × 122 mm, Avontuur A, 50 m Complex.

Fig. 3. *Patella hendeyi*. Holotype in dorsal view.
Scale = 30 mm.

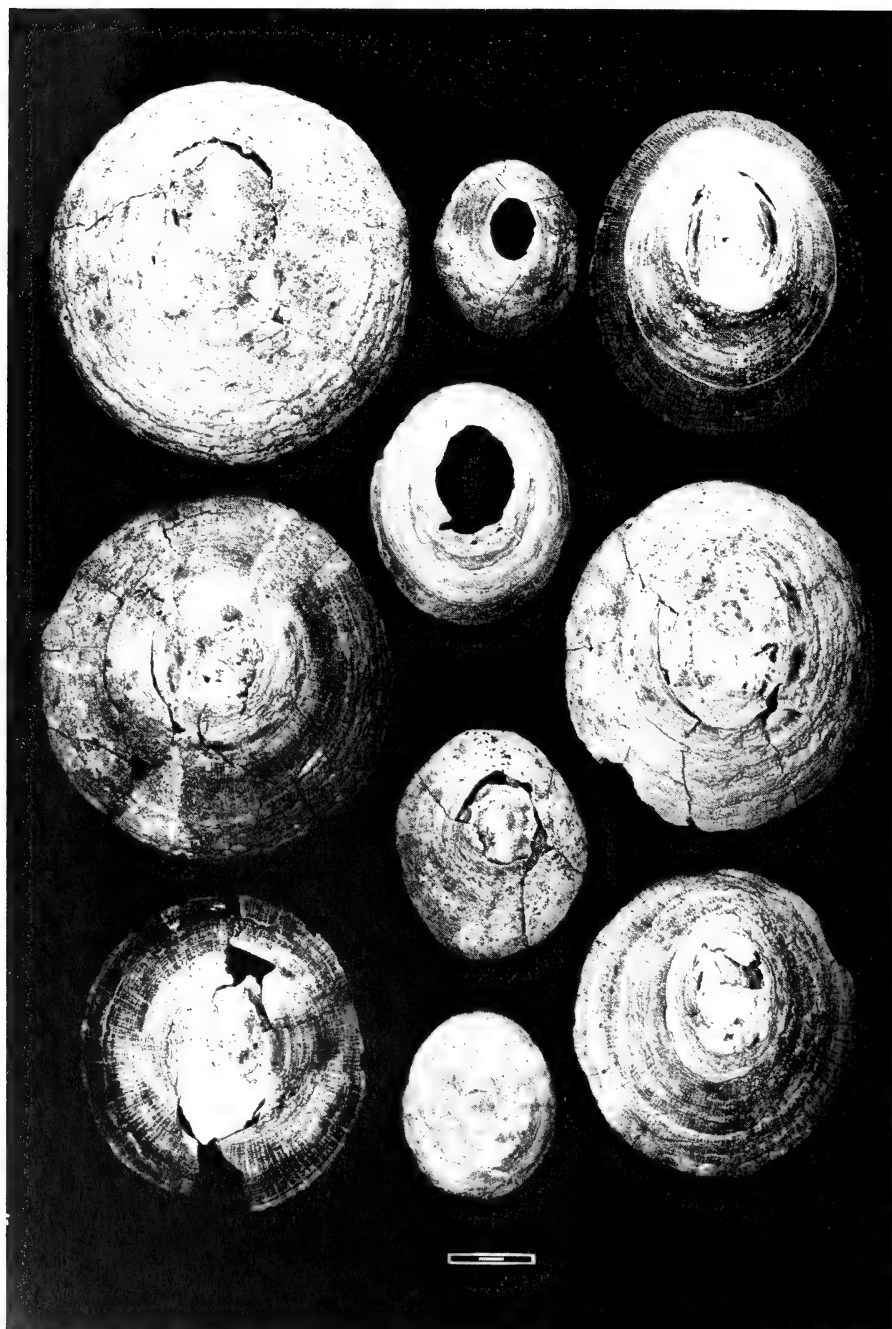


Fig. 4. *Patella hendeyi*. Holotype in upper right corner, remainder of specimens paratypes.
Scale = 30 mm.

Non-type material. SAM-PQ-AV459, 4 damaged and incomplete specimens, Avontuur A. SAM-9921, 2 specimens, 106×91 mm, 98×85 mm, Graauweduinen, Vanrhynsdorp District coast, Cape Province, coll. H. Harger. SAM-9932, 136×124 mm, Graauweduinen, Vanrhynsdorp District coast, coll. H. S. Harger.

Description

Shell heavy, relatively low, with subcircular outline, only slightly longer than wide, with apex anterior to midline, apex in all specimens eroded. Sculpture consisting of fine radial lines of subequal strength (about 300 on circumference of holotype, 200–300 in paratypes), becoming divided and/or distorted close to circumference. No juvenile scars on any specimens.

Remarks

The specimens numbered SAM-9921 and 9932 are those referred to by Haughton (1932: 30) as '*Patella* sp. (large)'.

Of present-day patellids living on the southern African coast, in terms of size, only *P. tabularis* Krauss, 1848, reaches the size of the largest specimen considered here. This species, however, characteristically has very large acute radiating ribs alternating with weaker ribs, and an irregular shell margin.

Patella safiana Lamarck, 1819, of West Africa has more regularly spaced but stronger ribs.

Patella argenvillei Krauss, 1848, has a narrower and higher shell.

Only very large shells of *P. granularis* Linnaeus, 1758, approach the present material in shape and sculpture. Prof. G. Branch (U.C.T.) has donated a specimen of *P. granularis* ($91,0 \times 74,9$ mm), that in shape closely resembles some of the smaller of the present fossils, and has faint radial sculpture as in the largest fossil. The possibility exists that *P. hendeyi* represents either a precursor of *P. granularis* or an earlier and much larger form of the same species.

Patella (Ancistromesus) fuenzalidai Herm, 1969, from the Pliocene of central Chile, bears a striking resemblance to the present species. The holotype and paratype of this species, at 209 mm and 188 mm length, are even larger than specimens of *P. hendeyi*, but have a very similar outline and general proportions and also the very fine radiating ribs seen in the Namaqualand species.

Etymology

The species is named for Dr Q. B. Hendey of the South African Museum.

Patella hoffmani sp. nov.

Figs 5, 6

Material

Holotype. SAM-PQ-AV508, $56,7 \times 51,0 \times 31,0$ mm (length \times width \times height), Avontuur A.

Paratypes. SAM-PQ-AV402, 9 specimens, $23,3 \times 18,9 \times 8,3$ mm; $32,3 \times 27,8 \times 10,6$ mm; $34,8 \times 31,4 \times 13,8$ mm; $42,9 \times 38,5 \times 15,8$ mm;

44,5 × 41,0 × 20,0 mm, 47,7 × 43,6 × 22,4 mm; 47,3 × 42,9 × 20,0 mm; 46,7 × 41,8 × 25,4 mm; 54,2 × 48,2 × 30,8 mm; Avontuur A. SAM-PQ-HB188, 48,4 × 41,2 × 27,1 mm, Hondeklip, 50 m Complex. SAM-PQ-HB191, 2 specimens, 48,5 × 41,9 × 23,0 mm; 51,6 × 45,8 × 26,7 mm; Hondeklip, 50 m Complex. SAM-PQ-HB142, 3 specimens, 39,7 × 32,0 × 18,7 mm; 46,9 × 38,8 × 21,7 mm; 47,7 × 40,2 × 25,6 mm; Hondeklip, 50 m Complex. SAM-K4755, 49,5 × 46,0 × 24,1 mm; Swartlintjies SL2, coll. A. J. Tankard. SAM-PQ-HB509, 3 specimens, 43,8 × 40,4 × 32,3 mm; 49,4 × 45,0 × 29,8 mm; 51,2 × 44,1 × 34,5 mm; Hondeklip Zone 4C, 50 m Complex. USNM 400980, 6 specimens, ? × 37,2 × 18,4 mm; 42,2 × 38,5 × 17,0 mm; 44,4 × 39,4 × 18,6 mm; 45,8 × 40,6 × 27,5 mm; 52,3 × 47,5 × 31,1 mm; 54,3 × 49,0 × 25,3 mm; Avontuur A, 50 m Complex.

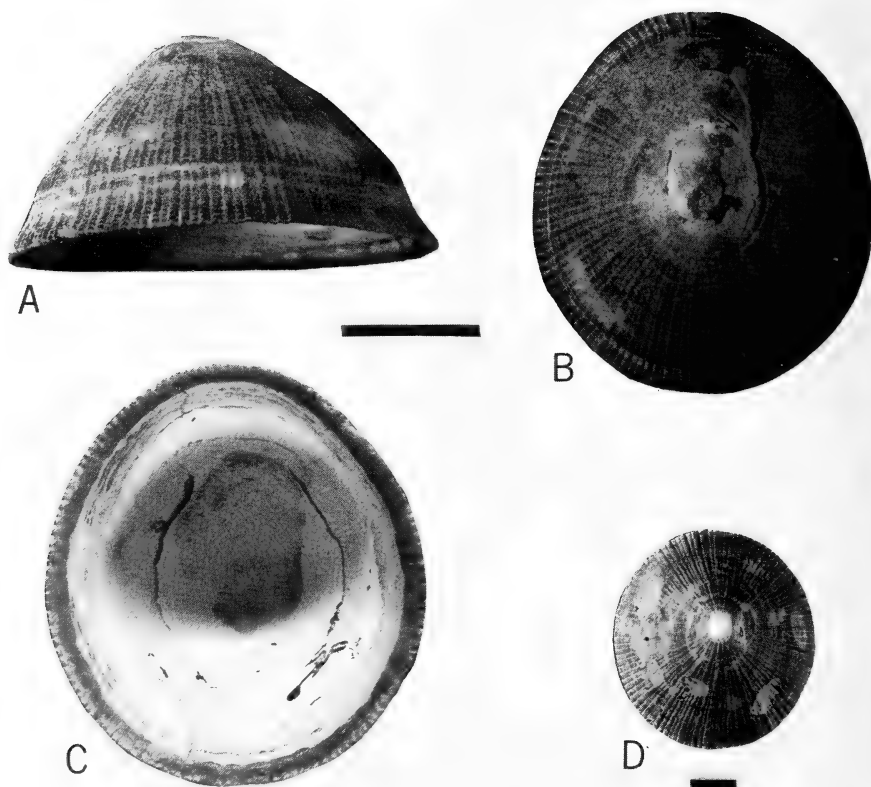


Fig. 5. *Patella hoffmani*. A-C. Lateral, dorsal and ventral views of holotype. Scale = 20 mm. D. Specimen showing juvenile scars. Scale = 10 mm.

Non-type material. SAM-PQ-HB249, 4 specimens, Hondeklip, B Block, 50 m Complex. SAM-PQ-AV402, 12 specimens, Avontuur A, 50 m Complex. SAM-PQ-AV510, 4 specimens, Avontuur A, 50 m Complex. SAM-K4754, 3 specimens, Koingnaas, coll. A. J. Carrington. SAM-K4756, 2 specimens, Somnaas SM4, 50 m, coll. A. J. Tankard. SAM-PQ-HB461, 27 specimens, Hondeklip, Zone 4C, 50 m Complex.

Description

Shell generally high-conical; length/width ratio range 80–93 per cent; sides very faintly convex; apex at or close to midpoint of antero-posterior line. Sculpture consisting of radiating flattened ribs of equal strength; under magnification, ribs seen to be built up of numerous concave growth lines,

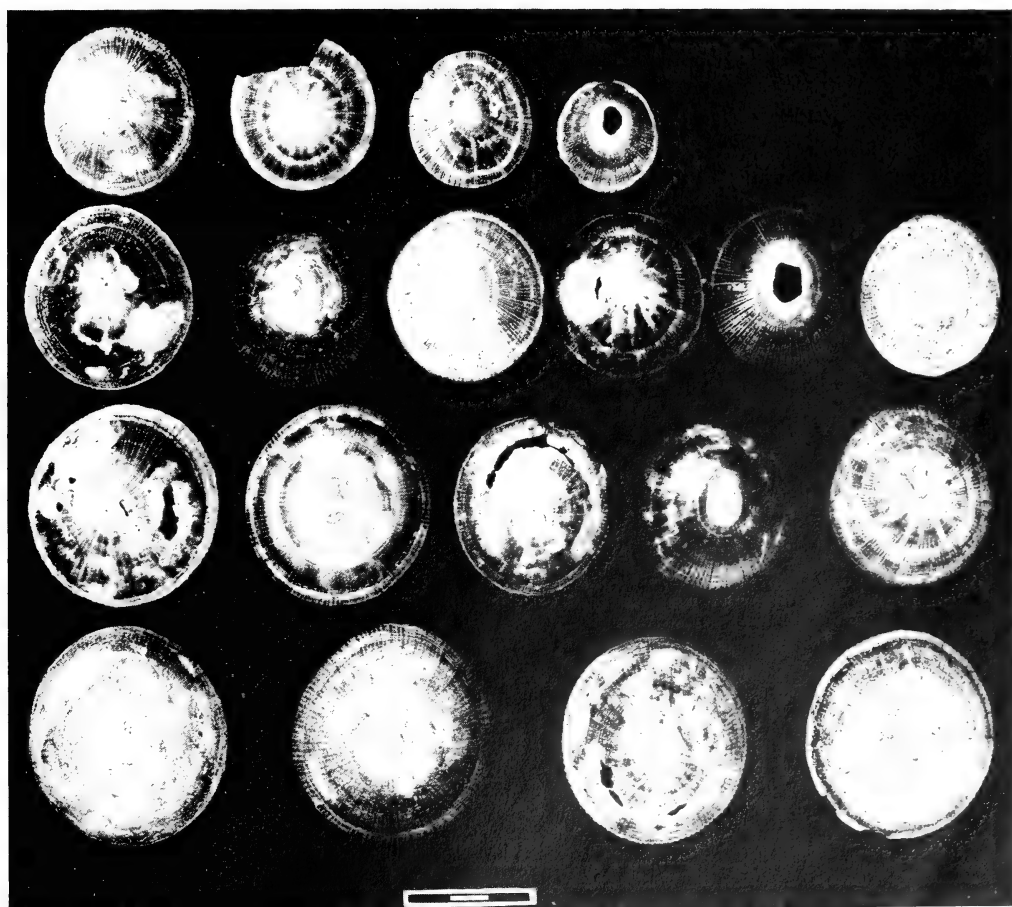


Fig. 6. *Patella hoffmani*. Range of specimens in dorsal view, some showing colour-rays. Scale = 30 mm.

somewhat flattened, separated by shallow sharp groove. Number of ribs on circumference of large specimens ranging from 105 to 124. Shell margin finely and evenly serrate. Large shells often with several oval juvenile scars, up to nine per shell; scars usually 4–10 mm greatest diameter. Some shells bearing dark-brown radiating bands separated by narrow pale bands; dark rays more distinct closer to shell apex; near margin, dark bands coalescing to form continuous dark-brown band.

Remarks

The almost circular circumference and tall conical shape of *Patella hoffmani* bears little resemblance either to any of the living or fossil southern or West African patellids. The sculpture of equal flattened radiating ribs, however, is almost identical to that of *Patella argenvillei*.

The subcircular and high-conical shape of *P. hoffmani* is reminiscent of *Nacella clypeater* (Lesson, 1831) from Chile. This species, however, possesses fewer radiating ribs which, unlike the flattened ribs of *P. hoffmani*, are low and rounded.

Etymology

The species is named for Mr F. Hoffman, of Transhex Pty Ltd diamond company.

Family Trochidae

Clanculus lutosus sp. nov.

Fig. 7

Material

Holotype. SAM-PQ-KN511, 16,3 × 18,3 mm, outer lip damaged, Koingnaas KN-1.

Paratypes. SAM-PQ-KN512, 5 specimens, Koingnaas KN-1.

Non-type material. SAM-PQ-KN513, 12 damaged specimens, Koingnaas KN-1.

Description

Shell top-shaped, of at least 4 postnatal whorls. Whorl profile straight to barely convex. Sculpture of spiral lines bearing bead-like, close-set tubercles; second whorl with 4–6 spiral lirae; third whorl with 10–12 lirae; body whorl with 10 lirae above shoulder, 12–14 on base. Shoulder narrowly rounded. Umbilicus broadly open, smooth, with single low spiral ridge. Columella with bipartite tubercle on lower portion. Outer lip slightly thickened, but lacking internal plicae.

Remarks

Clanculus murrayi has been described from the Quaternary of the Hondeklipbaai area (Carrington & Kensley 1969). This species, while having beaded



Fig. 7. *Clanculus lutosus*. Holotype. Scale = 10 mm.

spiral lirae as in *C. lutosus*, is characterized by a stepped profile, with two strong lirae on the whorl periphery.

Clanculus atricatena Tomlin, 1921, known from Transkei to Zululand, possesses a grooved lower tubercle on the columella, giving it a bipartite appearance. The spiral lirae of this species, however, are more finely beaded, while the outer lip possesses a strong posterior tubercle on the inner surface.

Clanculus kraussi Philippi, 1846, from West Africa, possesses finely beaded spiral lirae, but lacks the bipartite columella tubercle of *C. lutosus*. Two other West African species, however, show a stronger resemblance to the present material. *Clanculus santamariae* Gofas, 1984, from Benguela, Angola, has spiral lirae with fewer but larger beads, a crenulate umbilical opening, and a non-bifid columella tooth. *Clanculus pseudocorallinus* Gofas, 1984, also from Benguela, Angola, possesses sculpture very similar to that of *C. lutosus*, but also has a crenulate umbilical opening, and a non-bifid columella tooth. *Clanculus corallinus* (Gmelin, 1790) of the Mediterranean has fewer spiral lirae with larger beads, but does have a bifid columella tooth, and a non-crenulate umbilical opening as in *C. lutosus*.

Etymology

The specific name is derived from the Latin 'lutosus', muddy, and refers to the sediments from which the material was collected.

Gibbula zonata patula subsp. nov.

Fig. 8

Material

Holotype. SAM-PQ-HB514, 5,0 × 6,9 mm, body whorl damaged, Hondeklip Zone 3.

Paratypes. SAM-PQ-HB117, 4 specimens, 4,9 × 5,6 mm, 4,3 × 5,5 mm, 6,1 × 7,2 mm, 6,3 × ? mm, Hondeklip Zone 3. SAM-PQ-HB345, 6,8 × 6,5 mm, Hondeklip Zone 12.

Description

Shell broader than high, somewhat globular, of 4 whorls. Profile of whorls evenly rounded. Sculpture of rounded spiral bands; penultimate whorl with 6 bands; body whorl sculpture variable, with 8–10 bands on upper whorl; some specimens with intermediate finer lirae; ventral whorl with 8–12 lirae. Umbilicus broad, open in all specimens. Raised rounded bands in some specimens having darker colour than rest of shell.

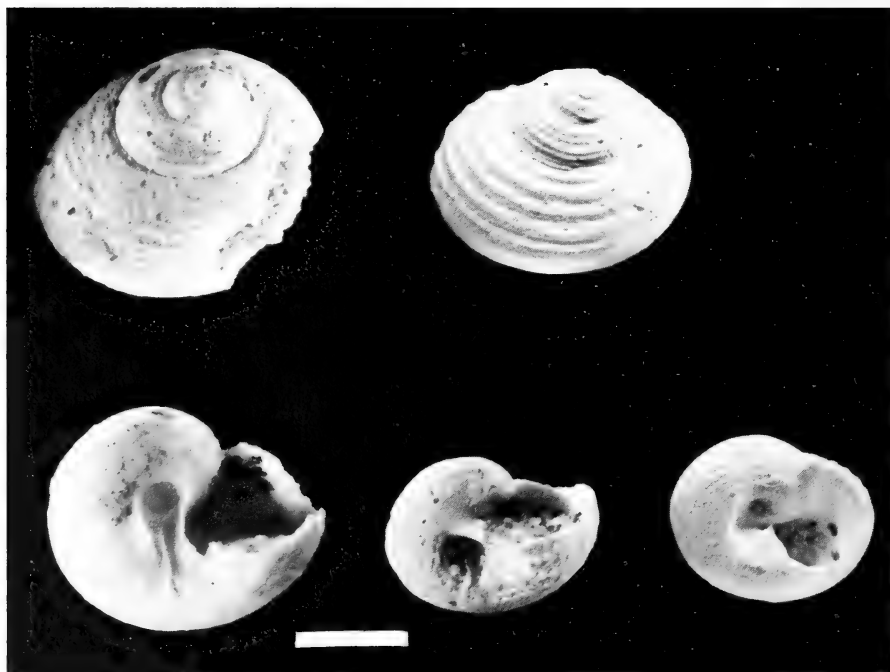


Fig. 8. *Gibbula zonata patula*. Holotype in upper left corner, remainder of specimens paratypes. Scale = 3 mm.

Remarks

The present material is very similar to *Gibbula zonata* (Wood, 1828), known from the intertidal and shallow infratidal of South West Africa–Namibia to False Bay, Cape. The variable spiral sculpture of the present material agrees well with the living species. The umbilicus is usually closed in adults, but occasionally remains open in the living species, while all the fossil specimens have open umbilici. As the fossils come from a distinctly warm-water assemblage, and *G. zonata* is characteristically a cold-water species, it seems essential to regard the fossil as a chrono-subspecies, or as a precursor species of *G. zonata*.

Etymology

The specific name derives from the Latin 'patulus', standing open, and refers to the open umbilicus of the species.

Family Turbinidae

Bolma anoropha sp. nov.

Fig. 9

Material

Holotype. SAM–PQ–KN516, operculum, length 23,2 mm, Koingnaas KN–1.

Paratypes. SAM–PQ–KN517, 6 opercula, lengths 17,6, 20,0, 25,0, 26,0, 26,1 mm, one damaged, Koingnaas KN–1. SAM–PQ–SL518, operculum, length 12,9 mm, Swartlintjies SL–20.

Description

Operculum narrowly elongate-oval, narrower at apical end; internal surface gently convex, with numerous growth-lines. Apex on outer ventral margin. External surface smooth, with rounded ridge in dorsal half. Operculum thickest posterodorsally.

Remarks

None of the living southern African turbinids possesses an operculum resembling the present material. *Bolma andersoni* (Smith, 1902), known from Transkei to Zululand, possesses a more broadly oval operculum, but has similar features, i.e. a smooth external surface, posterodorsally thickset, and with the apex on the outer ventral margin.

Unfortunately, no turbinid shell that could be associated with these opercula has been found in the deposits.

Etymology

The specific name, from the Greek 'anorophos', without a roof, alludes to the fact that no shell has been found associated with the present opercula.



Fig. 9. *Bolma anoropha*. Holotype in upper left corner, remainder of specimens paratypes. Scale = 10 mm.

Family **Turritellidae***Turritella declivis* Adams & Reeve, 1850

Turritella declivis: Barnard, 1963: 167, fig. 33c. Kensley, 1973: 74, fig. 243.

Material

SAM-PQ-KN350, numerous fragments, up to 47 mm in length, maximum diameter 13 mm, Koingnaas KN-1.

Previous records

Living: False Bay, 51 m; off Cape St. Francis, 12–112 m.

Dead: False Bay to Agulhas Bank, East London, 12–248 m.

No fossil record.

Remarks

Most of the present material is unworn, and shows the straight, even profile of typical *T. declivis*. A few fragments show slight development of a cingulum above the suture, but none show the hollowing of the whorls seen in the *T. excavata* form (see Barnard 1963: 168).

Family **Crepidulidae***Calyptraea kilburni* nom. nov.

Fig. 10

Calyptraea aurita striata Carrington & Kensley, 1969: 201, fig. 2c, pl. 22. Kilburn, 1980: 194.

Material

SAM-K1433 (holotype of *C. aurita striata*), 8,1 × 19,6 mm, Swartlintjies, 45–50 m transgression. SAM-PQ-HB148, 2 specimens, 9,8 × 27,2 mm, one damaged, Hondeklip HB-4, 50 m Complex. USNM 400981, 2 specimens,

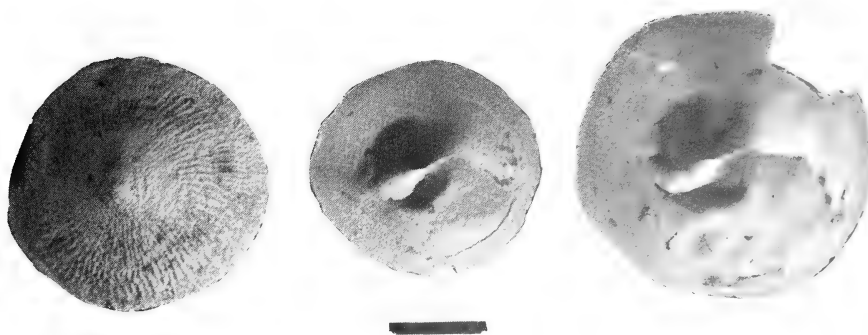


Fig. 10. *Calyptraea kilburni*. Left, dorsal view; centre and right, ventral view.
Scale = 10 mm.

9,0 × 23,3 mm, 11,4 × 30,4 mm, numerous fragments, Hondeklip, 50 m Complex.

Remarks

Kilburn (1980) correctly pointed out that the name '*striata*', used as a subspecific epithet by Carrington & Kensley (1969), was thrice preoccupied. Further, *C. aurita* (Reeve) from Chile differed markedly from the living South African species now named *C. barnardi* Kilburn, 1980. The west-coast fossil species, while having fine radiating striae similar to the Chilean *C. aurita*, differs in the structure of the septum. A new name is thus required for the Namaqualand fossil species.

Etymology

The species is named for Dr R. N. Kilburn of the Natal Museum, foremost southern African malacologist.

Crepidula deprima sp. nov.

Fig. 11

Material

Holotype. SAM-PQ-HB519, 22,6 × 9,2 mm, Hondeklip Zone 4A.

Paratypes. SAM-PQ-HB520, 2 specimens, 12,3 × 5,5 mm, 16,9 × 7,2 mm, 2 fragments, Hondeklip Zone 12. SAM-PQ-HB125, 1 specimen, 14,2 × 7,4 mm, Hondeklip HB-4. SAM-PQ-HB521, 3 specimens, 16,6 × 8,1 mm, 16,0 × 6,3 mm, 15,1 × 7,9 mm, 2 fragments, Hondeklip Zone 4A. USNM 400982, 1 specimen, 16,1 × 8,0 mm, 2 fragments, Avontuur A.

Description

Shell elongate-oval, strongly dorso-ventrally depressed, sides roughly parallel, anteriorly evenly rounded, dorsum convex in long axis, dorsal surface with irregular growth lines. Apex terminal on rounded posterior end. Ventral 'shelf' between posterior margin and start of septum. Free edge of septum evenly concave.

Remarks

Crepidula deprima bears little resemblance in its general shape and proportions to any of the southern or West African crepidulids. *Crepidula plana* Say, 1822, of the east coast of the U.S.A. is a similarly depressed species with a concave septum, but is much larger (up to 40 mm in length), with a narrowly rounded posterior end and a truncate anterior end.

Etymology

The specific name is derived from the Latin '*deprimo*', depressed, and refers to the dorso-ventrally depressed condition of the present species.

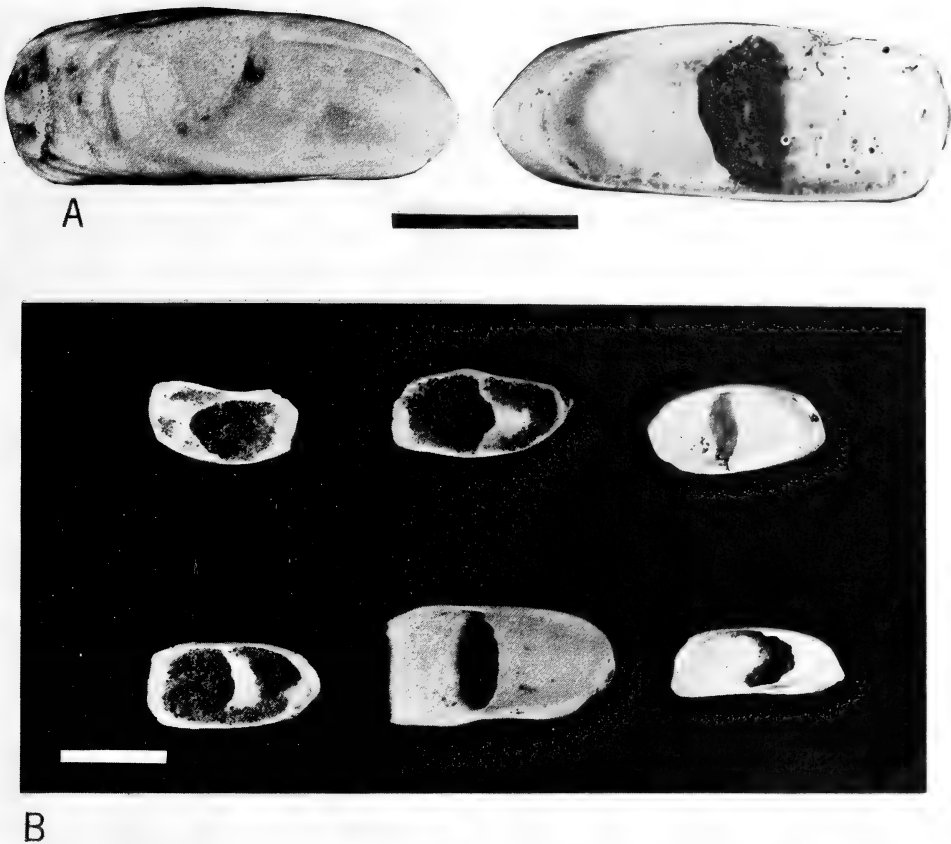


Fig. 11. *Crepidula deprima*. A. Holotype in dorsal and ventral view. B. Paratypes. Scales = 10 mm.

Family Naticidae

Natica cf. *andersoni* (Blainville, 1824)

Fig. 12

Natica adansonii (Blainville), Nicklés, 1950: 80, fig. 117.

Material

SAM-PQ-KN522, 8 specimens, ? \times 5,7 mm, 6,3 \times 6,4 mm, 15,8 \times 14,3 mm, ? \times 15,2 mm, 18,2 \times ? mm, 20,9 \times 17,8 mm, 20,4 \times 19,0 mm, 21,5 \times ? mm, Koingnaas KL south face.

Previous records

Living: Madeira; Cape Verde Islands; Morocco to Angola.

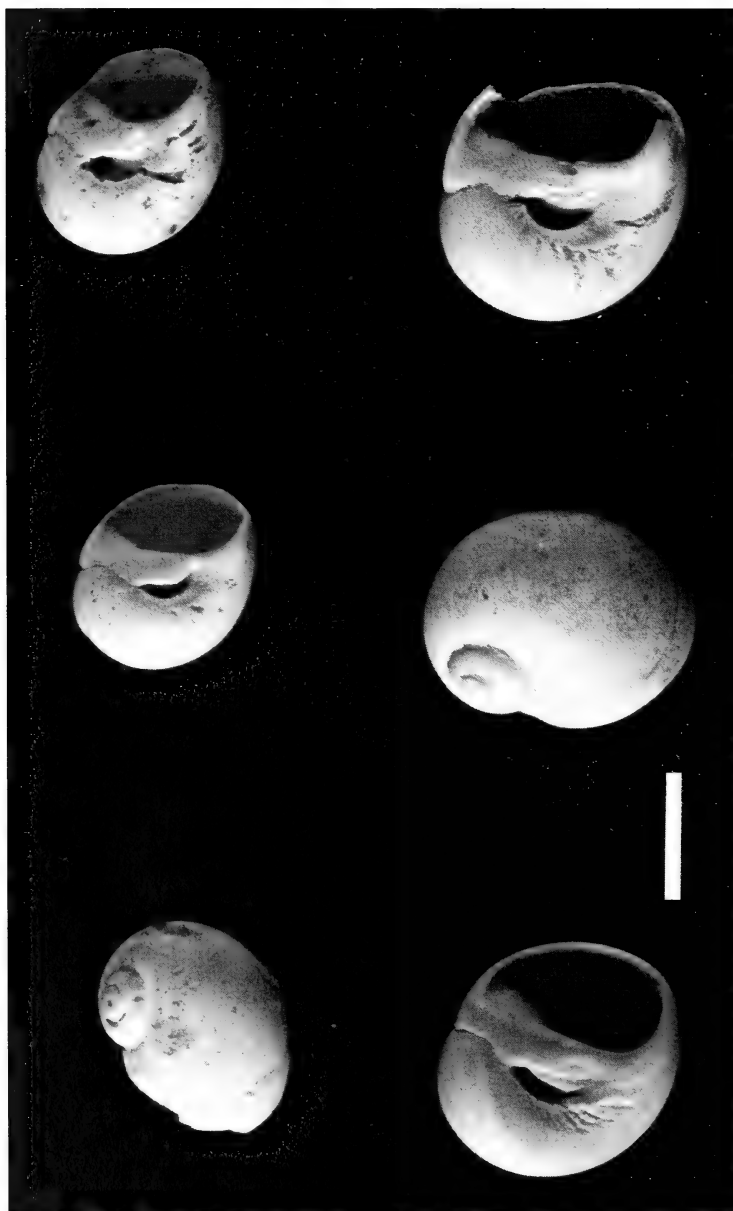


Fig. 12. *Natica* cf. *adansoni*. Scale = 10 mm.

Description

Shell slightly wider than long; spire low. Umbilicus with slight ridge at outer margin; columella callus forming convex lobe or bulge in umbilicus. Single specimen with broad band of brown pigment stretching from above umbilicus on to base and anterior end of outer lip.

Remarks

As all the present specimens are to some degree abraded, a definite identification is difficult. The form of the umbilicus, however, most closely resembles that of *N. adansoni*. The presence of a band of pigment around the umbilicus and base, typical of the living species, further suggests this identification.

Sinum concavum (Lamarck, 1822)

Fig. 13

Sigaretus concavus Lamarck, Nicklés, 1950: 81, fig. 121. Paes da Franca, 1960: 16.

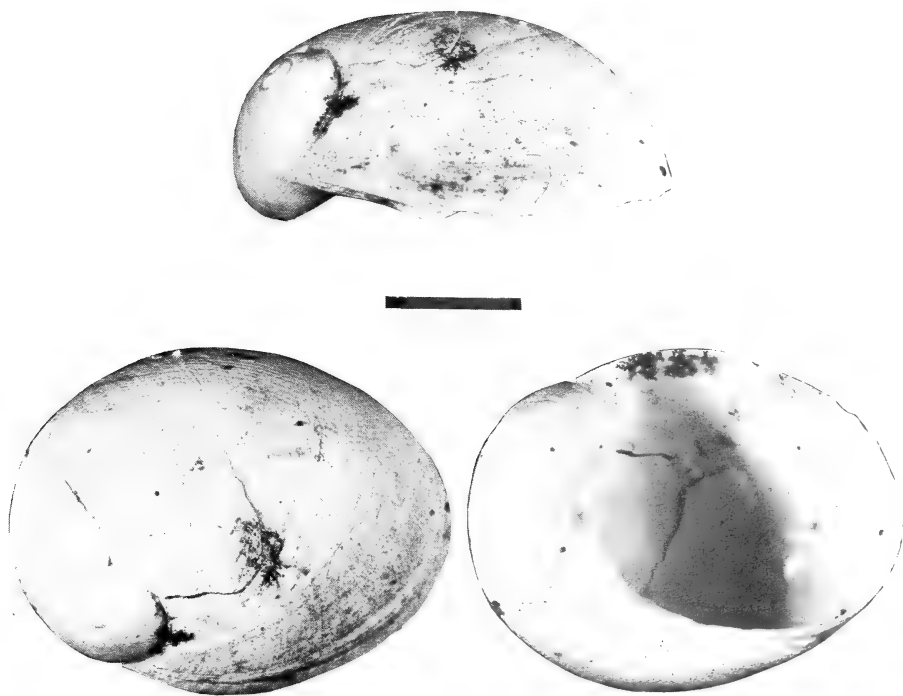


Fig. 13. *Sinum concavum*. Scale = 5 mm.

Material

SAM-PQ-HB515, longest diameter 16,8 mm, widest diameter 12,9 mm, Hondeklip B Block.

Previous records

Senegal to Moçâmedes, Angola.

Description

Shell thin, fragile. Protoconch indistinct; 4 postnatal whorls. Spire low, barely protruding above surface of body whorl. Sculpture consisting of low irregular flattened spiral lirae of varying widths, becoming obscure in columella area. Lirae +50 on body whorl, difficult to count as wider lirae tend to divide obscurely into several finer bands. Twenty-five lirae on penultimate whorl; obscure on earlier whorls.

Family Cymatiidae***Argobuccinum casus* sp. nov.**

Figs 14, 15

Material

Holotype. SAM-PQ-AV523, 89,9 × 50,9 mm, apex and base damaged; Avontuur A, 50 m Complex.

Paratypes. SAM-PQ-AV405, 3 specimens, 66,2 × 37,8 mm, 50,7 × 28,6 mm, 43,8 × 27,8 mm, Avontuur A, 50 m Complex. SAM-PQ-HB339, 4 specimens, 62,7 × 37,4 mm, 40,3 × 19,4 mm, 32,5 × 18,2 mm, 31,2 × 19,4 mm, Hondeklip Zone 12. SAM-PQ-AV524, 75,5 × 48,0 mm, 8 smaller specimens 48,8 × 21,9 mm to 29,0 × 15,8 mm, Avontuur A, 50 m Complex. USNM 400983, 2 specimens, 48,7 × 29,0 mm, 33,3 × 17,9 mm, Hondeklip Zone 12. USNM 400984, 58,9 × 32,9 mm, Avontuur A, 50 m Complex. USNM 400985, 4 specimens, 27,8 × 15,1 mm to 42,0 × 22,8 mm, Avontuur A, 50 m Complex.

Non-type material. SAM-PQ-AV525, 22 specimens, Avontuur A, 50 m Complex. SAM-PQ-HB526, 15 specimens, Hondeklip Zone 4A.

Description

Shell high-spined, very slightly dorso-ventrally compressed, with at least 5 postnatal whorls bearing a total of about 6 varices, latter not continuous from whorl to whorl. Profile of whorls evenly convex. Shell somewhat variable with regard to degree of elongation; few squatter specimens resembling *Argobuccinum pustulosum* (Lightfoot, 1786) in general proportions. Siphonal canal less than half length of aperture, slightly flexed to left. Outer lip with 11 or 12 ridges, becoming paired in older specimens. Columella smooth. Postnatal sculpture consisting of strong flattened spiral ridges or ribbons with narrow intervening grooves, 7 or 8 on earlier whorls, 13 to 15 on body whorl with finer alternating ridges appearing.

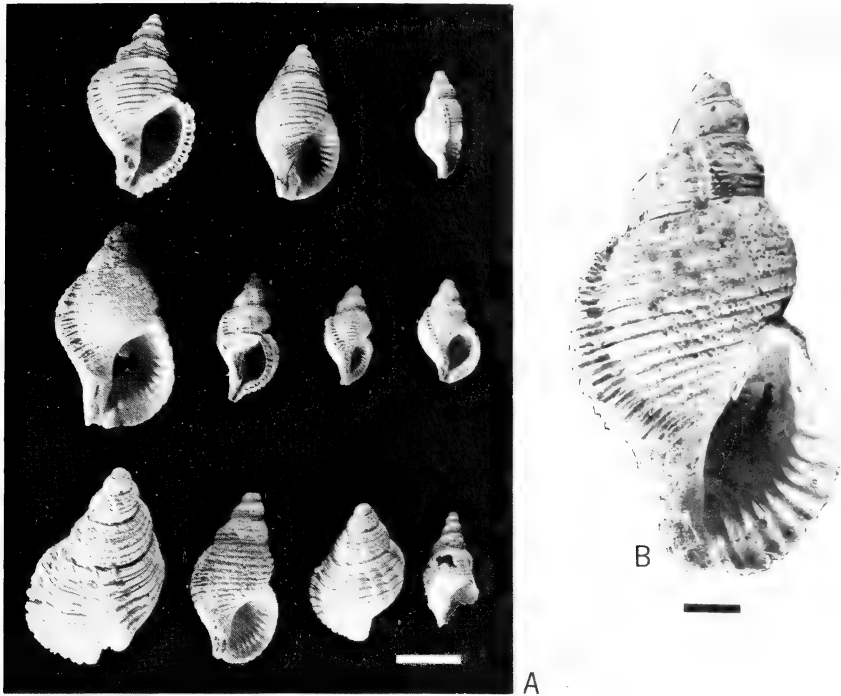


Fig. 14. *Argobuccinum casus*. A. Range of paratypes. Scale = 20 mm. B. Holotype. Scale = 10 mm.

Spiral ribbons becoming worn on body whorl, and seen to consist of 2 high ridges connected and covered by outer shell layer. Spiral ridges running on to dorsum of siphonal canal. Very faint rounded axial ridges seen in two specimens, 7 ridges between varices, becoming obsolete on body whorl.

Remarks

Of the cymatiids currently living on the west coast, *A. casus* most closely resembles *Argobuccinum pustulosum* (Lightfoot). This latter is said to occur in two forms or subspecies (see Kilburn & Rippey 1982: 75), with *A. pustulosum proditor* (Frauenfeld, 1865) being the west-coast form. *Argobuccinum casus* generally has a narrower shell even than this west-coast form, lacks the rounded tubercles on the spiral bands, has rounded tubercles rather than elongate ridges on the inner surface of the outer lip, has a more clearly defined siphonal canal, and lacks the short marginal digitiform projections of the lower outer lip. Even on the few specimens showing faint axial ribs, where these intersect the spiral bands, no rounded tubercles are formed as in the living species.

The present species was also compared with Pleistocene material of *A. pustulosum* (Lightfoot) from the Saldanha Bay area, and again, all the differences listed above are apparent.

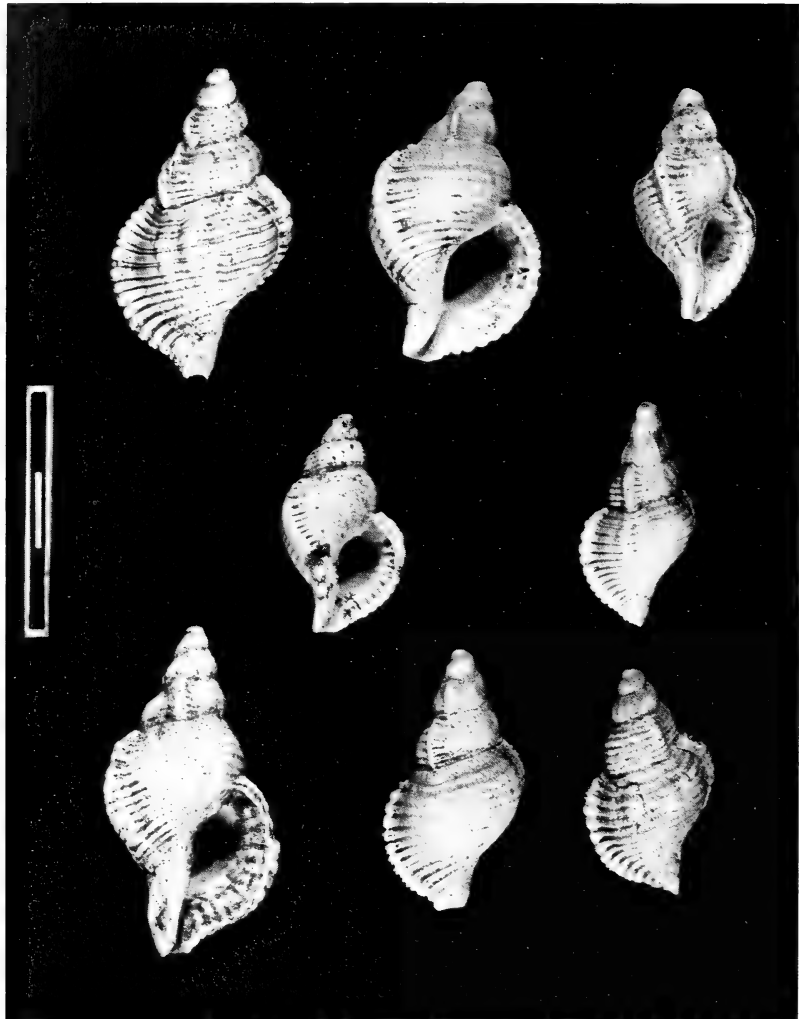


Fig. 15. *Argobuccinum casus*. Range of paratypes. Scale = 30 mm.

Cymatium parthenopeum (von Salis, 1793), living on the coasts of West and south-east Africa, and known as a fossil from the Pliocene of Italy, possesses fewer spiral bands, but stronger axial sculpture than *A. casus*.

Etymology

The specific name, the Latin for 'adventure', is derived from the farm-name Avontuur, a locality for the present species as well as several others described in this work.

Family Epitoniidae

Epitonium (Gyroscala) lycocephalum sp. nov.

Fig. 16

Material

Holotype. SAM-PQ-HB527, 14,5 × 6,6 mm, Protoconch damaged, Hondeklip Zone 4A, 50 m Complex.

Paratypes. SAM-PQ-HB528, 2 specimens, 13,0 × 5,0 mm (apex missing), 12,9 × 4,6 mm, Hondeklip Zone 12, 50 m Complex.

Non-type material. SAM-PQ-HB529, 15 fragments, Hondeklip A Block, 30 m Complex.

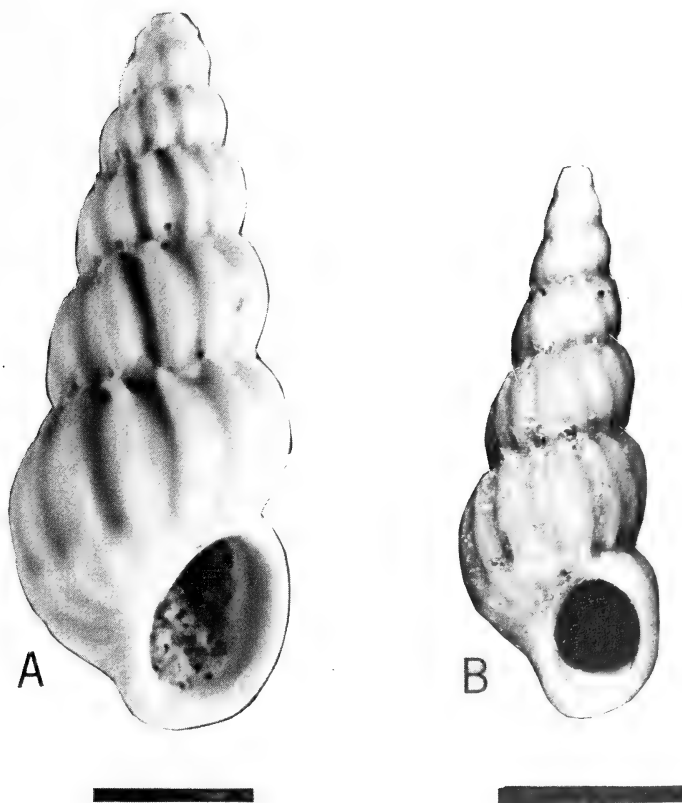


Fig. 16. *Epitonium lycocephalum*. A. Paratype. Scale = 3 mm.
B. Holotype. Scale = 5 mm.

Description

Protoconch unknown; at least 6 postnatal whorls. First whorl with 12–13 well-defined rounded lamellae; second to fifth whorls each with 15 lamellae; body whorl with 14 lamellae. At least 20 very fine spiral lines visible between lamellae, becoming obscure near upper and lower sutures, and difficult to count. Strong basal lira on body whorl. Suture crenulate. Outer lip varicoid.

Remarks

The present material resembles the living east-coast species *E. coronatum* (Lamarck, 1816) in the possession of a basal lira, but is more slender. The common *Epitonium* of the west coast, *E. kraussi* (Nyst), lacks both spiral lirae and a basal lira. *Epitonium lamellosum* (Lamarck, 1822) of West and South Africa is a somewhat broader shell, with fewer lamellae (9–10 on body whorl), and lacks distinct spiral sculpture.

Etymology

The specific name, from the Latinized Greek meaning 'wolf head', alludes to a low hill or koppie, Wolfkop, in the vicinity of Hondeklip Bay.

Family **Thaididae***Nucella praecingulata* (Haughton, 1932)

Figs 17, 18

Thais praecingulata Haughton, 1932: 48, pl. 5 (figs 6–10). Barnard, 1958: 219; 1962: 182.*Material*

Syntypes. SAM-9730, 3 specimens, Reuning's Claim, Alexander Bay, Cape Province, coll. J. B. Cilliers. SAM-10598, 1 internal mould, The Point, Namaqualand coast, Cape Province, oyster horizon, coll. E. Reuning. SAM-9731, 4 specimens, Alexander Bay; SAM-9742, 1 specimen; SAM-9743, 1 specimen; SAM-9745, 1 specimen; SAM-9746, 1 specimen; SAM-9749, 1 specimen; SAM-9750, 1 specimen; SAM-9752, 1 specimen; SAM-9753, 1 specimen; SAM-9754, 1 specimen; SAM-9934, 7 specimens; all previous specimens from Graauweduinen, Vanrhynsdorp District coast, Cape Province, unless otherwise stated, coll. S. Haughton.

Non-type material. SAM-PQ-AV398, 18 specimens, 18–58 mm, Avontuur A, 50 m Complex. SAM-PQ-HB344, 28 specimens, 16–57 mm, Hondeklip Zone 12. SAM-PQ-HB334, 5 specimens, 81–110 mm, Hondeklip Zone 12. SAM-PQ-KN460, 2 specimens, 103 mm, 110 mm, Koingnaas, 50 m Complex.

Description

Shell thaidid-like, variable, with aperture longer than spire. Protoconch of 1–1½ whorls, apparently smooth (but all specimens apically somewhat eroded); 4+ postnatal whorls, generally with well-marked shoulder. Spire in relation to body whorl variable, squat in some specimens and half length of aperture, to

more slender and three-fourths length of aperture. Sculpture variable, squatter specimens generally with stronger sculpture; early whorls with 4 strong spiral bands and numerous axial lamellae between bands and upper and lower suture lines, giving cancellate appearance. Spiral bands increasing on to body whorl, with intermediaries appearing in some specimens; up to 20 major spiral bands, running on to base. Cancellation usually lost on body whorl. Specimens having weaker spiral sculpture usually with shoulder marked by single somewhat stronger band; sculpture in these specimens often becoming obsolete on body whorl. Columella smooth, concave in lower half. Base rounded, fasciole strong. Inner surface of outer lip generally plicate, folds becoming obsolete in larger specimens.

Remarks

Barnard (1962: 182) noted that *Nucella praecingulata* resembles both *Nucella cingulata* (Linnaeus, 1758) and *N. squamosa* (Lamarck, 1816), but reaches a much greater size than either of these living species.

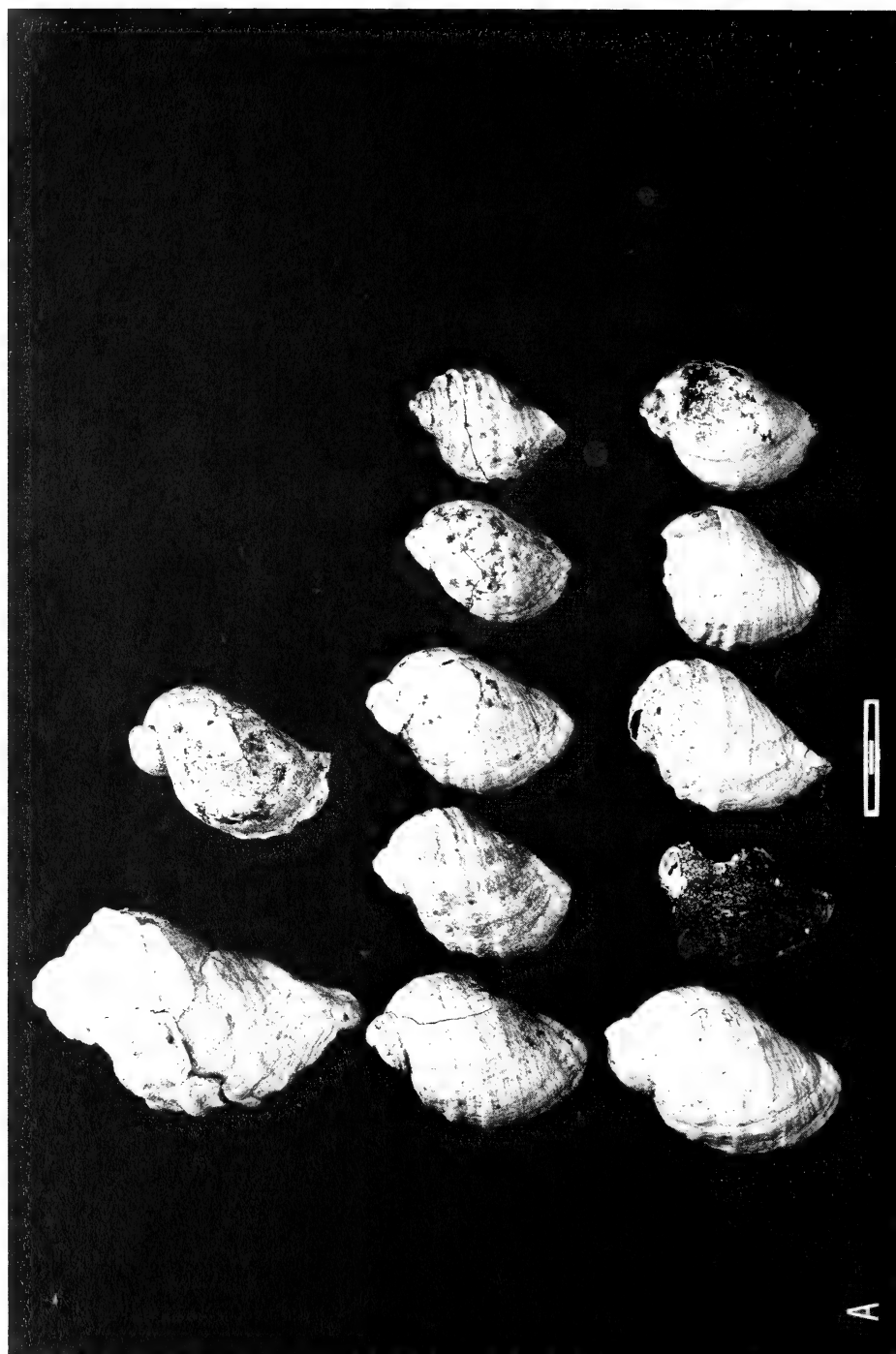
Haughton (1932) quotes a note from Tomlin, in which the latter suggests the name 'praecingulata', and also observes the similarity to *N. cingulata* and *N. squamosa*. Haughton, while not presenting a formal description, noted the variability of the species, did not designate a holotype, but saw all the material listed above under 'Syntypes' (Fig. 17).

In spite of being highly variable, large specimens of *N. praecingulata* (approx. 100 mm) are easily identified, being the only whelk of such dimensions in the west-coast deposits. Smaller specimens, in the size range of *N. cingulata* and *N. squamosa*, however, are more difficult to assign.

In the majority of smaller specimens of *N. praecingulata* the body whorl and at least the two earlier whorls have a faint but distinct shoulder on the upper part of the whorl. The strength of the spiral bands varies. In those specimens in which the spiral bands are few and strong, the resemblance to *N. cingulata* is unmistakable, even to the possession of five axial lines between the spiral bands, leading to the squamose appearance sometimes seen in *N. cingulata*. In these specimens, the whorls tend to have an evenly rounded profile. In those specimens in which the spiral bands are finer and more numerous, the axial lines lead to a cancellate appearance very similar to *N. squamosa* (see Fig. 19). In these, the slightly angular whorl profile is more apparent, but even here, evenly rounded whorls are encountered.

It is suggested that with the change to a colder regime on the west coast during the Pleistocene, *Nucella praecingulata* gave rise to two forms, *Nucella cingulata* and *N. squamosa*, both being intertidal to shallow infratidal forms, neither attaining the dimensions of the ancestor, and with *N. cingulata* being confined to the colder waters of the west coast to False Bay, while *N. squamosa*, perhaps with greater temperature tolerance, extends to the Transkei coast.

Nucella praecingulata has not been recorded concurrently with *N. cingulata* or *N. squamosa*, a further indication of the form's possible ancestral role.



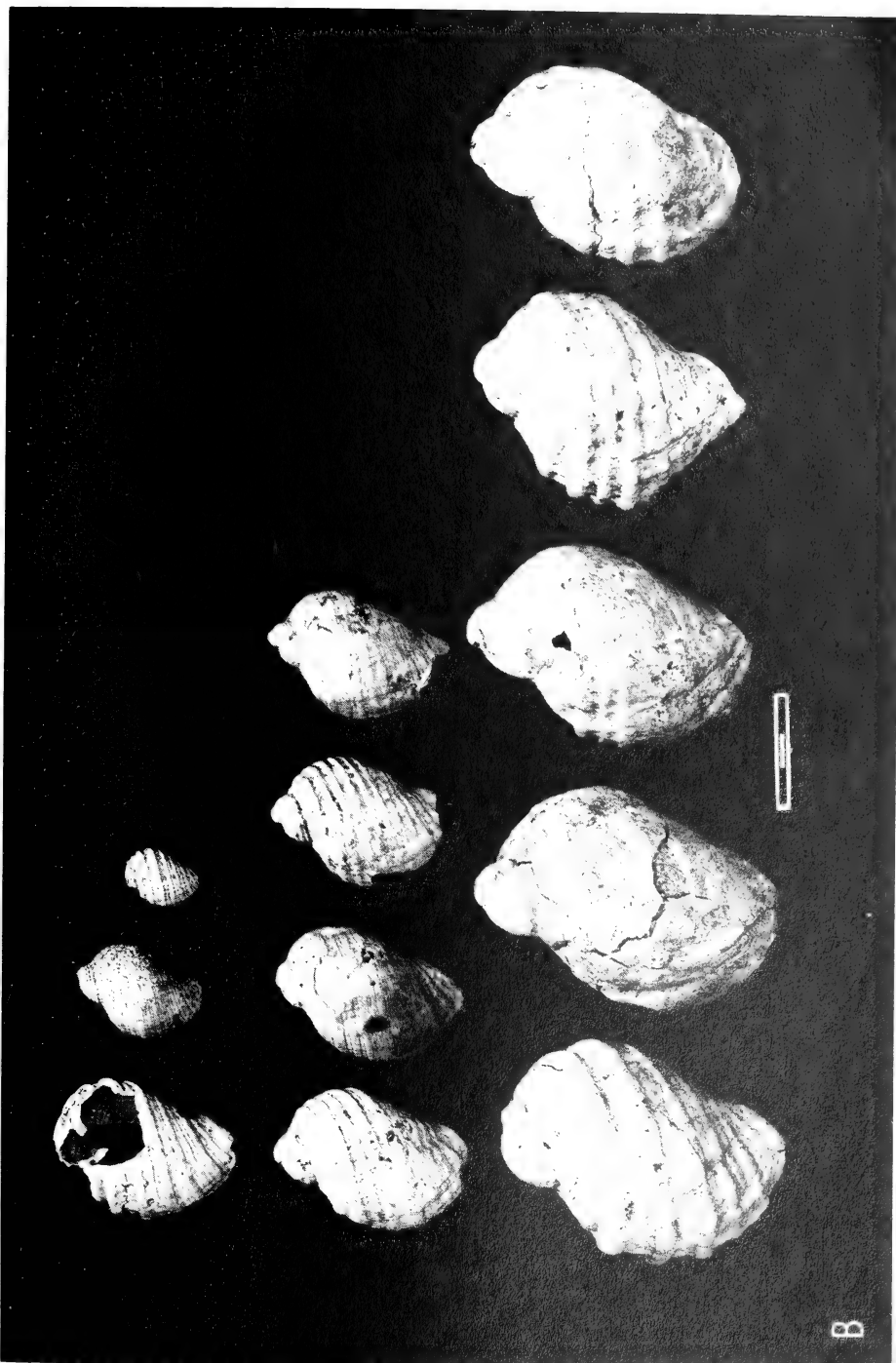
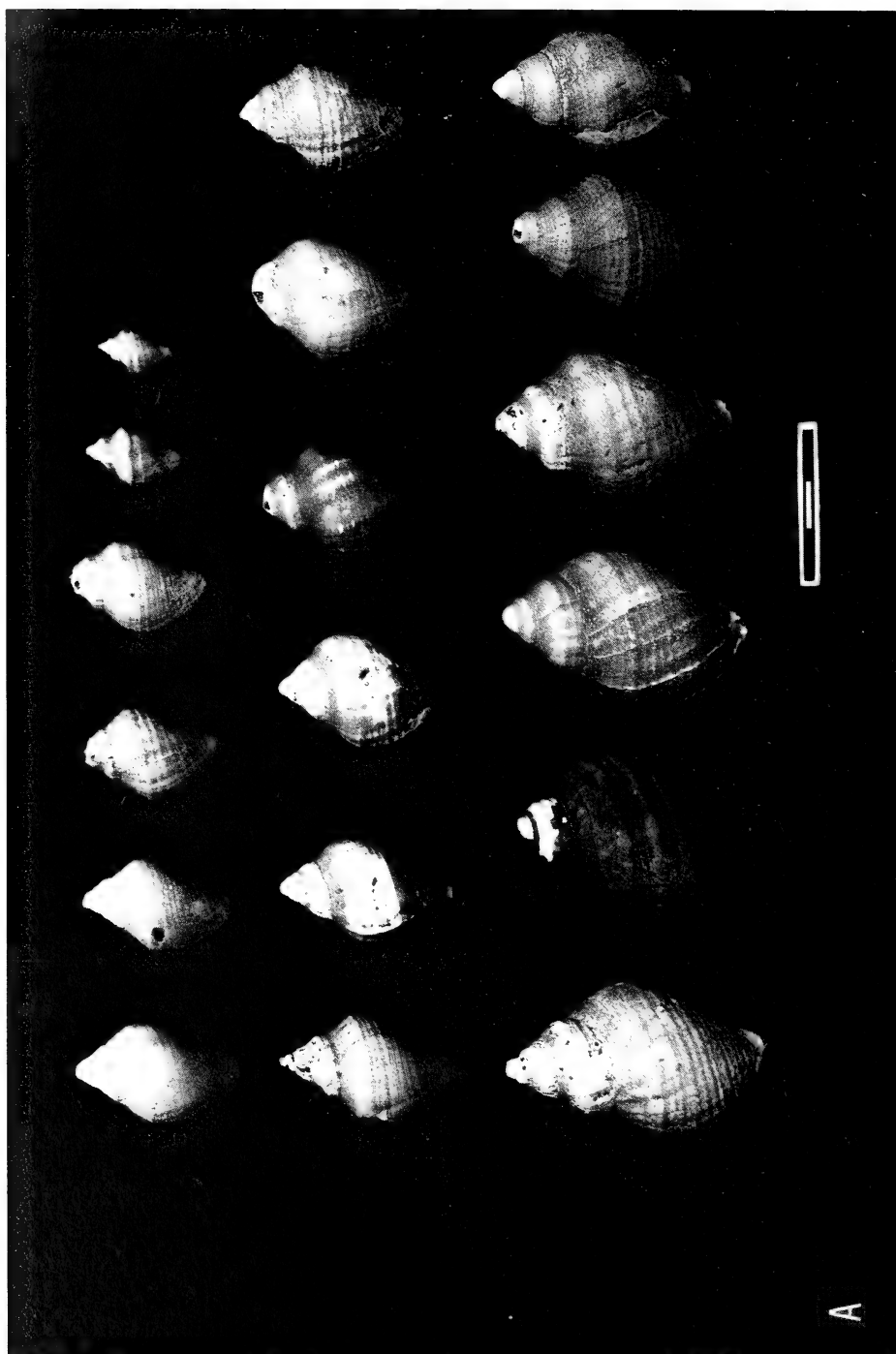


Fig. 17. *Nucella praecingulata*. A, B. Syntypes. Scale = 30 mm.



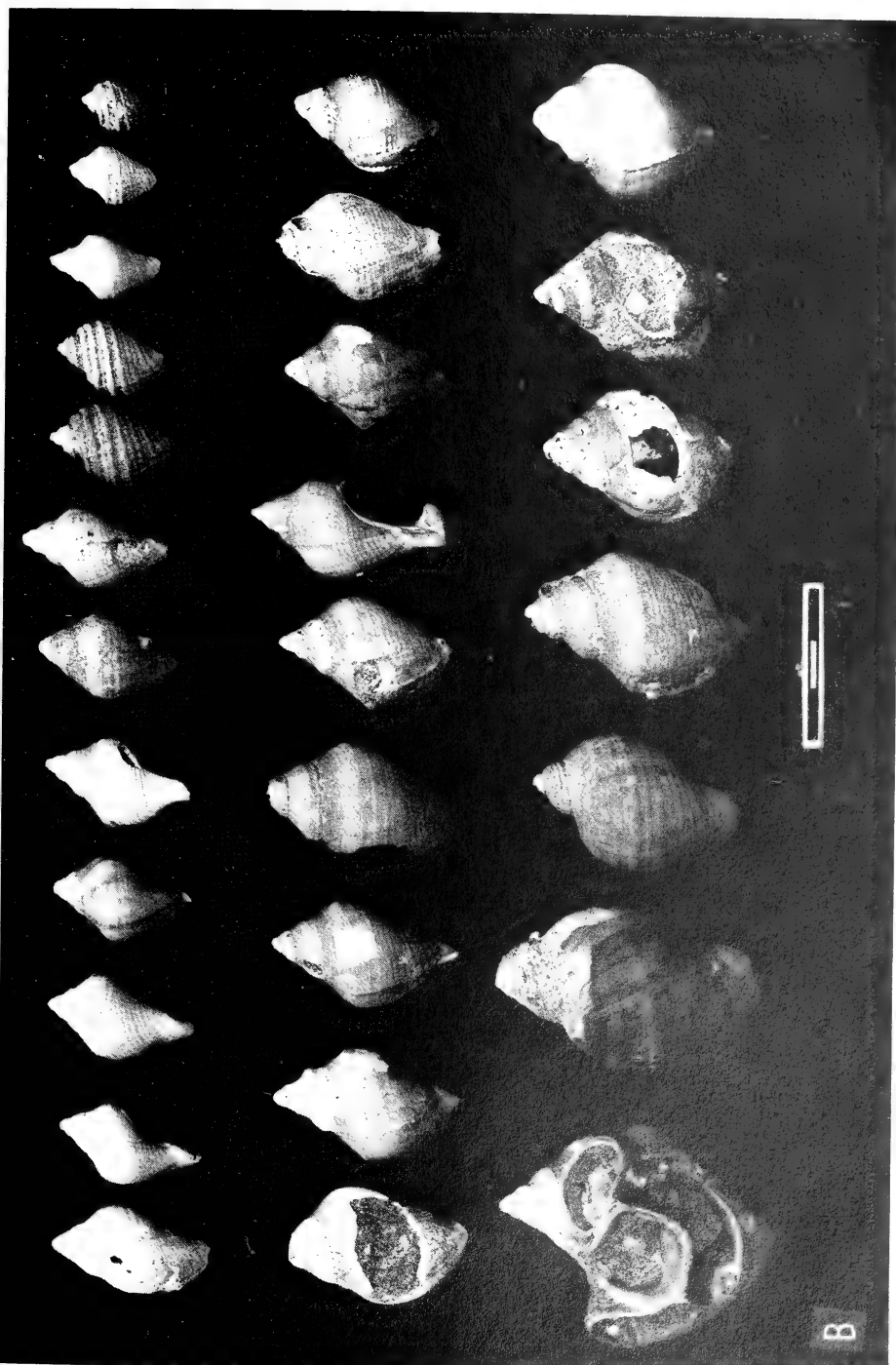


Fig. 18. *Nucella praecingulata*. A. Avontuur specimens. Scale = 30 mm. B. Hondeklip specimens. Note oyster shells on lower left specimen. Scale = 30 mm.

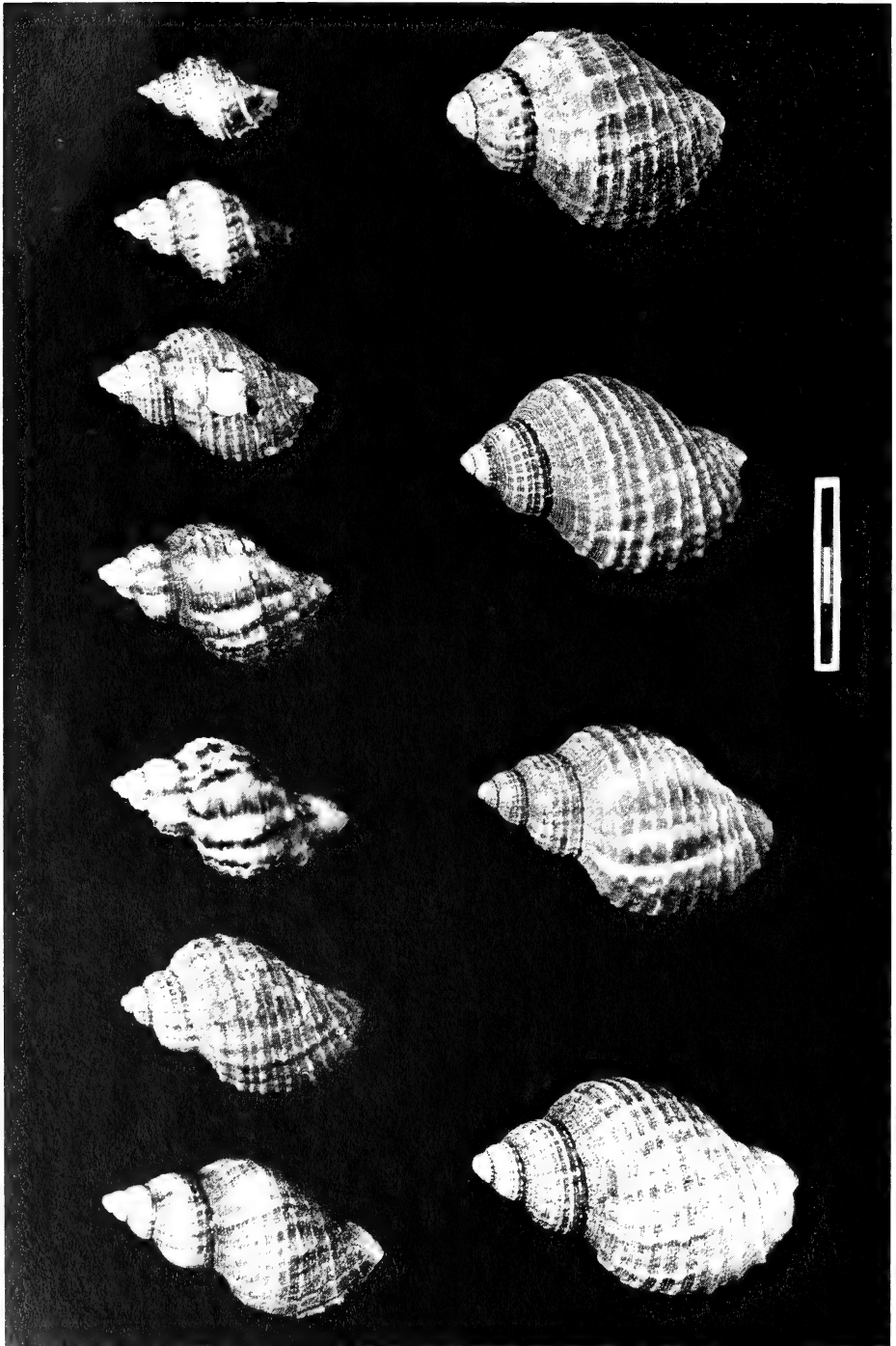


Fig. 19. *Nucella squamosa*. Recent specimens from Cape Peninsula and False Bay. Scale = 30 mm.

Thais arenae sp. nov.

Fig. 20

Material

Holotype. SAM-PQ-KN530, almost complete specimen, length 52,5 mm, greatest width 27,3 mm, Koingnaas KL south face.

Non-type material. SAM-PQ-KN307, 3 fragments (body whorls, somewhat worn), Koingnaas KL south face.

Description

Shell with at least 4 postnatal whorls; aperture longer than spire. (The holotype, an almost complete specimen, lacks the tip of the spire.) Whorls with distinct shoulder in upper half. Columella smooth; short anterior canal flexed slightly to left. Second extant whorl with 14 axial ribs, spiral sculpture worn away. Third whorl with 11–12 axial ribs, 2 strong spiral keels, upper forming shoulder; axial ribs rounded at intersections with strong keels; fine spiral sculpture over entire whorl, 11–12 lirae between suture and shoulder, 9–10 below shoulder.



Fig. 20. *Thais arenae*. Holotype. Scale = 10 mm.

Body whorl with 10 axial ribs, becoming obsolete on outer lip; 5 strong keel-like spiral bands; 12–13 fine lirae between suture and shoulder; 10–12 fine lirae between each strong spiral band; 4 fine lirae between lowest band and base.

Remarks

The present species bears some resemblance to *Thais capensis* (Petit, 1852), especially in the fine spiral lirae, but the latter is a relatively squatter species having somewhat stronger tubercles, especially on the body whorl. *Thais haemastoma* (Linnaeus, 1767), especially in the form occurring at present at the southern end of its West African range, has a much squatter shell bearing variable rounded tubercles on the shoulder, rather than the rounded ribs of *T. arenae*.

Lathyrus armatus A. Adams (see Nicklés 1950: 106) from the Azores, the Canary Islands, and Senegal, has a similar overall shape and sculpture. Although the holotype of *T. arenae* shows some wear on the axial ridges and tubercles, these are still more rounded than in the West African species. Also, the anterior canal is more defined in the latter species.

Etymology

The specific name, from the Latin, of a sandy place, refers to the coarse sands of the type-locality at Koingnaas KL south face.

Family Muricidae

Ocenebra bonaccorsii (Carrington & Kensley, 1969)

Tritonalia bonaccorsii Carrington & Kensley, 1969: 196, pl. 19.

Material

SAM-PQ-HB531, 39,1 × 22,0 mm, Hondeklip A Block, 30 m Complex. SAM-PQ-HB532, 2 specimens, 8,4 × 4,8 mm, 8,1 × 4,0 mm, Hondeklip Zone 12, 50 m Complex. SAM-PQ-HB152, 22,1 × 10,8 mm (protoconch missing), Hondeklip Zone 3.

Remarks

The PQ-HB531 specimen above is both larger and better preserved than the holotype. The description of the species can thus be supplemented:

Protoconch of 2–2½ whorls; 4½ postnatal whorls. First two postnatal whorls bicarinate; third whorl with upper carina stronger than lower; postnatal whorl 2 with 4 fine spiral lirae between suture and upper carina, 2–3 fine lirae between upper and lower carina; 2–3 lirae between lower carina and suture. Postnatal whorls 3 and 4 with 8–9 lirae between upper suture and upper carina; 4–5 lirae between carinae; 4 lirae between lower carina and lower suture. Body whorl with 13–15 lirae between upper suture and strongest spiral ridge; 8 strong spiral ridges, 9 fine lirae between uppermost strong ridge and next, number of fine lirae decreasing anteriorly to two or three between stronger ridges. Inner surface of outer lip with 8 rounded ridge-teeth.

Ocenebra petrocyon sp. nov.

Fig. 21

Material

Holotype. SAM-PQ-HB533, 9,9 × 4,8 mm, Hondeklip, 30 m Complex.

Paratypes. SAM-PQ-HB534, 10,6 × 5,7 mm, 8,6 × 4,6 mm; Hondeklip, 30 m Complex. SAM-PQ-HB535, 5 damaged specimens, 20 juvenile specimens; Hondeklip A Block, 30 m Complex.



Fig. 21. *Ocenebra petrocyon*. Holotype at left, remainder of specimens paratypes. Scale = 3 mm.

Description

Protoconch of $1\frac{1}{2}$ smooth whorls; 4 postnatal whorls. Aperture subequal to, or slightly longer than, spire. Sculpture consisting of rounded axial ribs and spiral lirae. Axial ribs: 11–12 on first whorl; 11–12 on second whorl; 11 on third whorl; 11 on body whorl. Spiral lirae: 4 on first whorl; 5 on second whorl; 5 on third whorl; 5 (with 1 or 2 very fine intermediates) on fourth whorl; 18–20 on body whorl (outer lip), including several finer intermediates; lirae running on to anterior canal. Lirae somewhat broadened at intersection with axial ribs, but never becoming bead-like. Narrow, smooth columella callus present. Inner surface of outer lip with 8–10 faint spiral ribs.

Remarks

Ocenebra petrocyon most closely resembles *O. purpuroides* (Reeve, 1845) (with which it was collected), especially in general shape and body-whorl sculpture. The new species differs from *O. purpuroides* in that the upper two or three whorls are not cancellate; in having more spiral lirae per whorl; in having spiral lirae evenly spaced between the upper and lower suture lines (*O. pur-*

puroides has a distinct shoulder and no lirae between shoulder and the upper suture line); and in having the axial ribs more rounded (almost carinate in *O. purpuroides*).

Etymology

The specific name is the Latinized form of the Greek for 'dog stone', and alludes to the farm Hondeklip.

Trophon carringtoni sp. nov.

Fig. 22

Latiaxis sp. Carrington & Kensley, 1969: 195, pl. 19.

Material

Holotype. SAM-PQ-AV536, 42,5 × 22,5 mm, Avontuur A, 50 m Complex.

Paratypes. SAM-PQ-AV537, 2 specimens, 37,1 × 22,4 mm, 40,8 ×

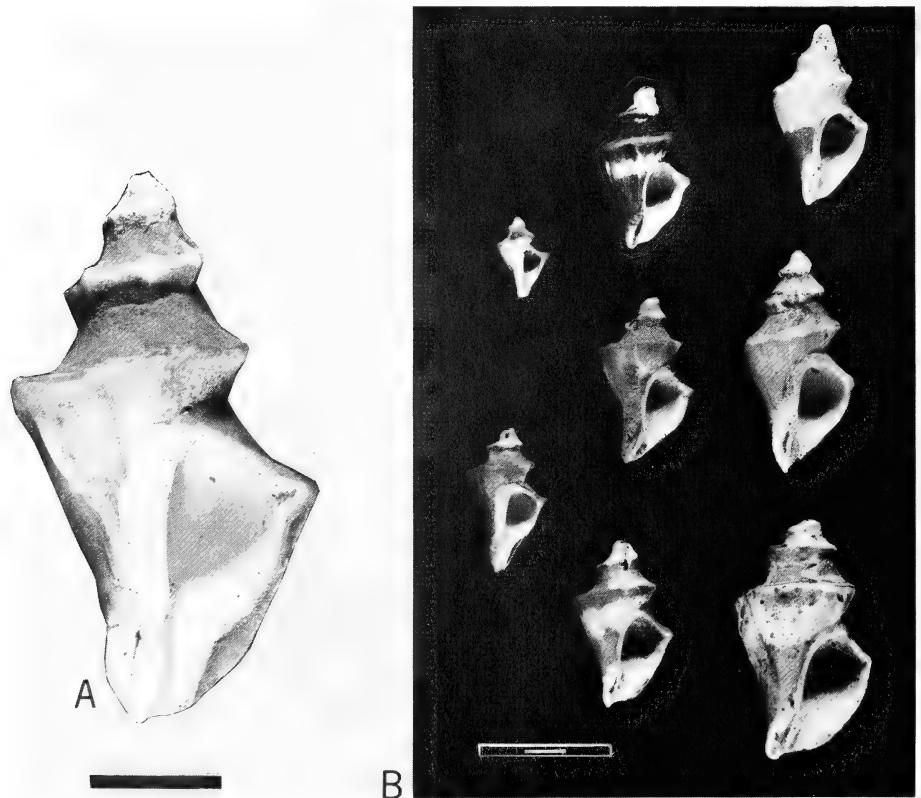


Fig. 22. *Trophon carringtoni*. A. Holotype. Scale = 10 mm. B. Range of paratypes. Scale = 30 mm.

24,5 mm, Avontuur A, 50 m Complex. SAM-K1447, 62,5 × 37,0 mm, outer lip missing, Strandfontein, 45–50 m Complex, coll. A. J. Carrington. SAM-PQ-AV538, 8 specimens (all with eroded apices), 58,0 × 32,0 mm, 53,0 × 28,0 mm, 42,5 × 23,5 mm, 40,2 × 24,0 mm, 40,0 × 23,5 mm, 38,2 × 22,0 mm, 34,8 × 20,0 mm, 20,0 × 13,0 mm, Avontuur A, 50 m Complex. USNM 400986, 3 specimens (all with eroded apices), 42,0 × 24,8 mm, 43,0 × 23,3 mm, 38,0 × 25,9 mm, Avontuur A, 50 m Complex.

Description

Shell of 4–5 postnatal whorls; aperture longer than spire. Whorls with single prominent keeled shoulder. Early whorls with irregular axial ridges, giving appearance of cancellate sculpture below keel, forming more or less well defined squamae where keel intersected. In later whorls, 6–8 axial ridges only faintly indicated above keel, stronger below keel, especially on body whorl, forming faint swelling at intersection with keel. Columella smooth, with callus developed. Inner surface of outer lip with 5 tubercles below carinal notch. Short anterior canal flexed to left.

Remarks

In the original mention of this species (Carrington & Kensley 1969: 195) the resemblance to *Latiaxis tortilis* (= *L. nakamigawai* io Kilburn, 1974) was mentioned. This comparison no longer stands, as the present species is more slender, does not have a strongly flexed anterior canal, and appears to lack spiral sculpture, other than the carina.

The general shape and sculpture are reminiscent of members of the Trophoninae, but resemble nothing recorded in the southern African fauna.

Etymology

The species is named for Mr A. J. Carrington of De Beers Consolidated Diamond Mines.

Family Buccinidae

Burnupena rogersi sp. nov.

Fig. 23

Material

Holotype. SAM-PQ-HB539, 58,1 × 34,5 mm (body whorl plus 2½ whorls, remainder of spire missing), Hondeklip Zone 3, 50 m Complex.

Paratypes. SAM-PQ-HB540, 14 specimens, 48,3 × 30,5 mm to 14,7 × 8,7 mm (larger specimens with outer lip and/or body whorl damaged and spire missing; smaller specimens complete). Hondeklip Zone 3, 50 m Complex. USNM 400987, 5 specimens, 38,4 × 24,3 mm to 15,7 × 8,9 mm, Hondeklip Zone 3, 50 m Complex.

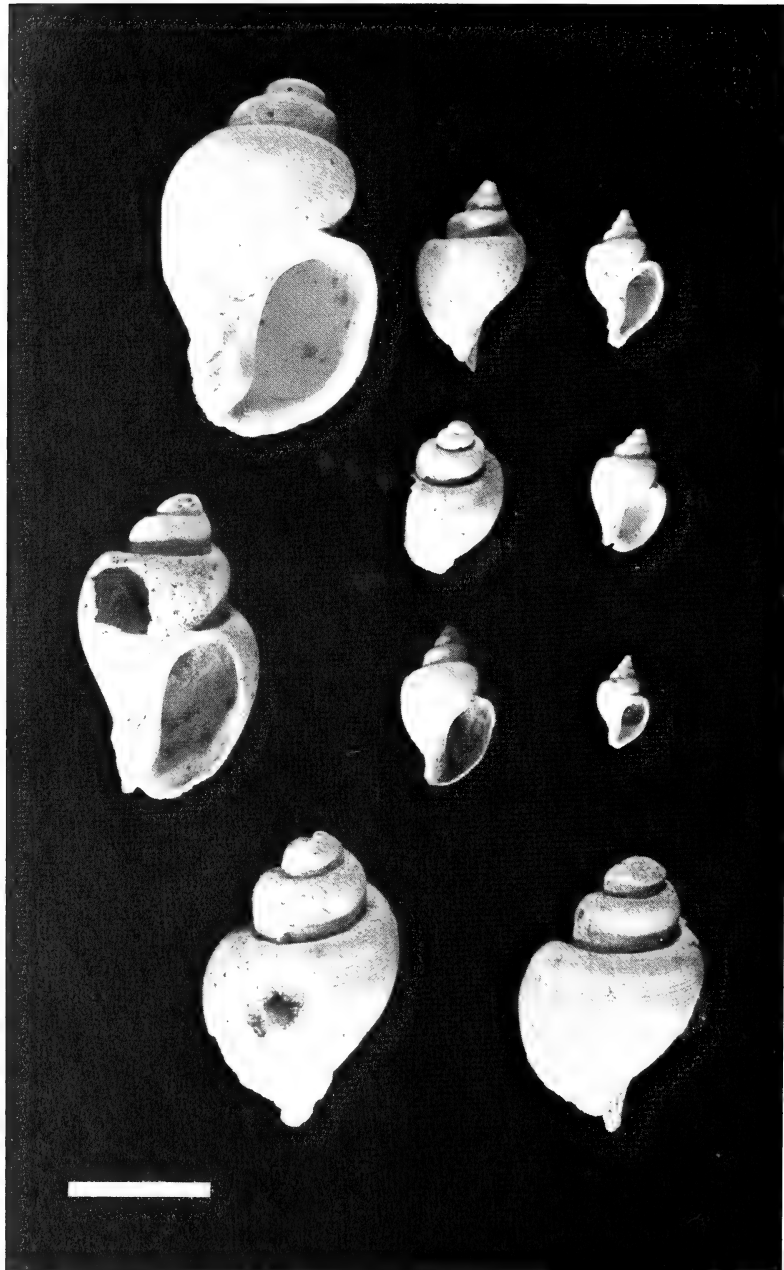


Fig. 23. *Burnupena rogersi*. Holotype at upper left corner, remainder of specimens paratypes. Scale = 20 mm.

Description

Shell about 1,5 times longer than wide. Protoconch unknown; at least 5 postnatal whorls. Profile of earlier whorls evenly convex; of last 3 whorls with distinct, rounded shoulder. Sculpture of fine spiral bands separated by narrow incised grooves; 7–8 on third from last whorl, 14–15 on penultimate whorl, 35–42 on body whorl, extending on to outer surface of anterior canal, flattened bands becoming obscure, divided by shallow incised lines on lower body whorl. No axial sculpture apart from faint growth lines, and several aperture margin ridges in larger specimens. Narrow gutter formed at suture line on last whorl, becoming closed on earlier whorls. Inner surface of outer lip with about 10 faint ridges. Base narrowly umbilicate; columella lacking pleats; with weak callus; anterior canal short, flexed slightly to left.

Remarks

The present material, showing a strongly sunken suture, bears some resemblance to the genus *Babylonia*. *Burnupena rogersi*, however, is plumper than the two South African species of *Babylonia*, neither of which possesses fine spiral sculpture.

While the generic position of the present material cannot be established in the absence of radula, soft parts, and operculum, the species does bear a general resemblance to species of *Burnupena*, and especially to *B. papyracea* (Bruguière, 1789), which sometimes does show a fairly sunken suture.

Etymology

The species is named for Dr John Rogers of the Department of Geology, University of Cape Town.

Burnupena aestus sp. nov.

Figs 24, 25

Material

Holotype. SAM-PQ-AV541, 69,9 × 31,0 mm, Avontuur A, 50 m Complex.

Paratypes. SAM-PQ-AV542, 3 specimens, 62,4 × 30,3 mm (apex and outer lip damaged), 67,1 × 29,9 mm, 68,4 × 32,0 mm, Avontuur A, 50 m Complex. SAM-PQ-HB543, 76,6 × 29,7 mm (apex damaged), Hondeklip Zone 12, 50 m Complex. SAM-K1445, 61,3 × 27,0 mm (body whorl damaged), Swartlintjies, coll. A. J. Carrington, 1967. SAM-K1446, 67,1 × 34,6 mm (body whorl damaged), Swartlintjies, coll. A. J. Carrington, 1967.

Description

Shell elongate, relatively slender, spire longer than aperture. At least 5 postnatal whorls. Profile of whorls convex, with slight hollowing just below suture. Columella smooth, basally flexed slightly to left, with rounded ridge just

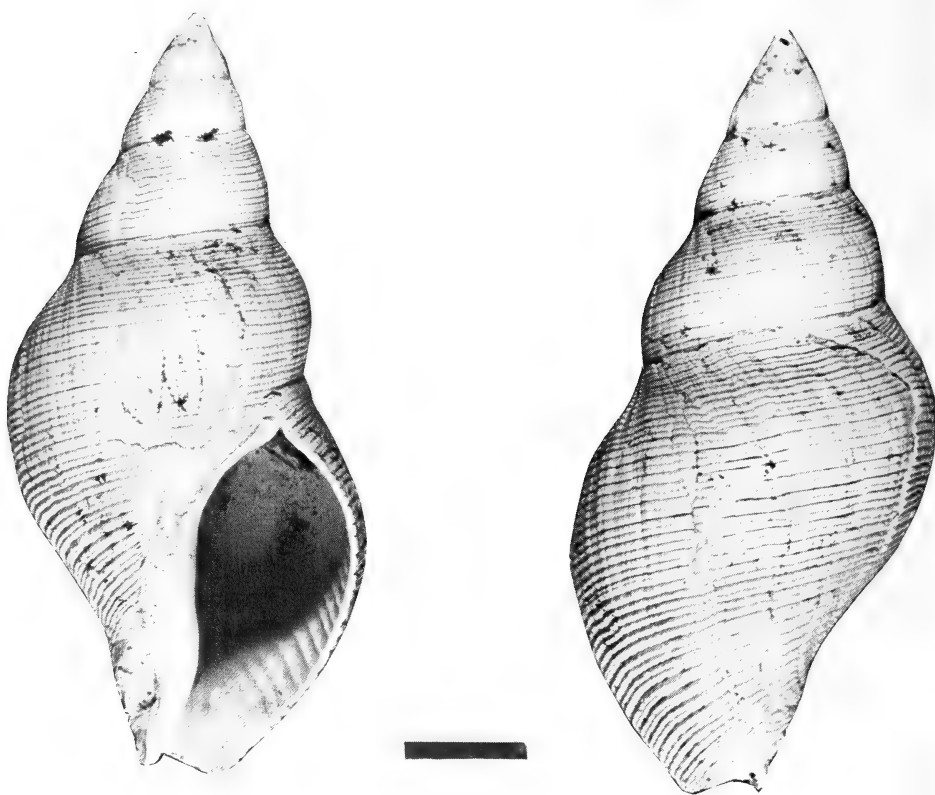


Fig. 24. *Burnupena aestus*. Holotype. Scale = 10 mm.

below suture; base rounded. Inner surface of outer lip with 20–22 rounded ridges. Sculpture consisting of fine spiral lirae, occasionally doubled on lower whorls; spiral lirae narrowly rounded to carinate. Second whorl with 10–12 lirae; third with 12–15; fourth with about 20; body whorl with up to 56 lirae.

Remarks

In general proportions, the present species most resembles *Afrocominella capensis* (Dunker, 1844), but lacks the obscure axial sculpture of the early whorls typical of this species. The spiral lines are finer and more numerous than in *A. capensis*, while the aperture is generally subequal in length to the spire. The present species attains a much larger size than either *A. capensis* or *Burnupena papyracea*, the other species to which it bears some similarity. This latter species is much squatter, with fewer spiral lines.

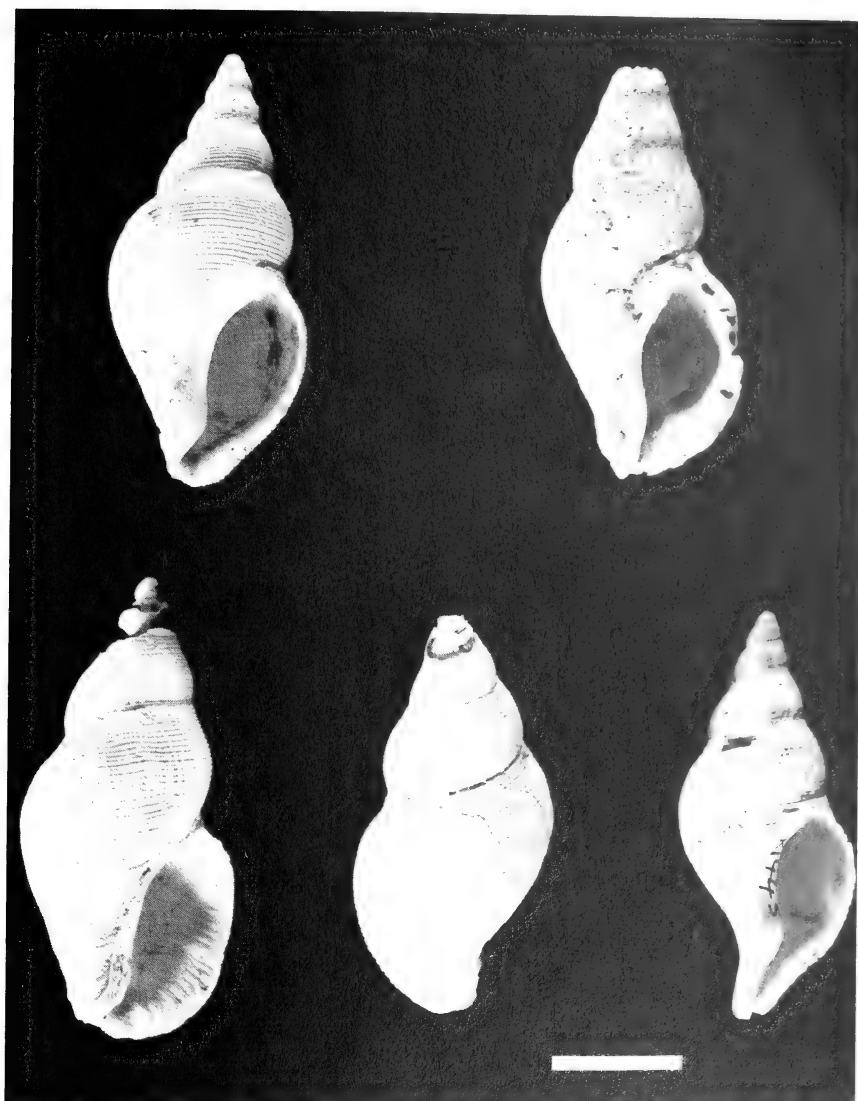


Fig. 25. *Burnupena aestus*. Paratypes. Scale = 20 mm.

There is a possibility of confusing small specimens of this species with large specimens of *Triumphis dilemma* (see below). The two species may, however, be easily separated on the following features: columella smooth in *B. aestus*, with 2–4 tubercles in *T. dilemma*; aperture longer than spire in *T. dilemma*, shorter than spire in *B. aestus*; outer lip frequently thickened in *T. dilemma*, unthickened in *B. aestus*; spiral cords on body whorl and anterior canal often doubled,

normally rounded to carinate in *B. aestus*, spiral cords single, rounded to tabulate in *T. dilemma*.

Etymology

The specific name is derived from the Latin 'aestus', of the surf, and refers to the probable habitat of the species.

Triumphis dilemma Kilburn & Tankard, 1975

Fig. 26

Triumphis dilemma Kilburn & Tankard, 1975: 200, fig. 10.

Material

Holotype. SAM-K4565, 16,3 × 10,4 mm, Langebaan, Early Pleistocene, coll. A. J. Tankard.

Non-type material. SAM-PQ-HB544, 10 specimens, 27,2 × 17,8 mm to 39,1 × 22,0 mm, Hondeklip Zone 4A, 50 m Complex. SAM-PQ-AV545, 6 specimens, 25,3 × 15,0 mm to 33,0 × 19,9 mm, Avontuur A, 50 m Complex. SAM-K4862, 4 specimens (2 damaged), 24,9 × 13,2 mm, 30,9 × 16,3 mm, Somaas SN4, Hondeklip Bay, coll. A. J. Tankard.

Previous records

Early Pleistocene, Langebaan, 9,5 m beach.

Remarks

With a wider range of material available, the original description can be supplemented: parietal area with single tooth in most cases; 2 teeth (as in holotype) only very occasionally seen. Outer lip only occasionally not thickened; with 10–17 internal ridges. Columella with 2–5 basal tubercles, 2 most common. Spiral cords rounded to tabulate. Aperture longer than spire, generally not as constricted as in holotype. Kilburn & Tankard (1975) mentioned two damaged specimens considerably larger than the holotype, about which they had reservations. With good material in this size range, it can be seen that the two earlier specimens are in fact this species, and that the higher counts of spiral cords are typical of the species.

Family Nassariidae

Bullia annulata (Lamarck, 1816)

Bullia annulata: Barnard, 1959: 127, figs 25f, 27e; 1962: 189.

Bullia magna Haughton, 1932: 46, pl. 5 (figs 1, 4, 5). Barnard, 1959: 129; 1962: 182, 189.

Material

SAM-9897 (syntypes of *B. magna*), 2 incomplete specimens, Graauwe-duinen, Vanrhynsdorp District coast, Cape Province. SAM-7998, (syntypes of *B. magna*), 16 incomplete specimens, Doornbaai, south of Olifants River mouth,

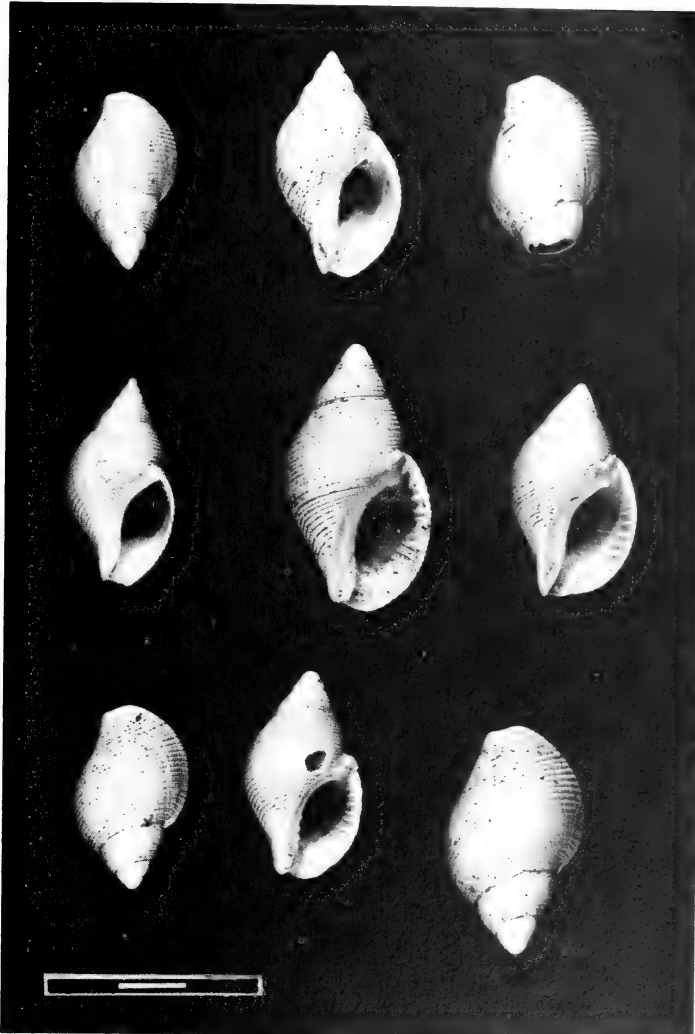


Fig. 26. *Triumphis dilemma*. Range of material from Hondeklip, 50 m Complex. Scale = 30 mm.

Cape Province. SAM-K4863, 1 specimen, $67,6 \times 32,2$ mm, Swartlintjies SL2, Hondeklip Bay, coll. A. J. Tankard. SAM-PQ-HB210, 3 specimens, $63,7 \times 30,1$ mm, $68,7 \times 32,2$ mm, $55,6 \times ?$ mm (body whorl incomplete), Hondeklip Zone 12, 50 m Complex. SAM-PQ-AV233, 7 specimens (3 incomplete), $64,3 \times 30,7$ mm, $60,8 \times 30,8$ mm, $59,9 \times 30,3$ mm, $51,2 \times 26,9$ mm, Avontuur, 50 m Complex. SAM-PQ-AV588, 12 specimens, Avontuur, 50 m Complex. SAM-PQ-HB613, 1 specimen, Hondeklip Zone 4A, 50 m Complex. SAM-PQ-HB889, 2 specimens, Hondeklip Zone 12, 50 m Complex.

Remarks

Barnard (1962) expressed the view that *Bullia magna* was merely a worn and fossilized *B. annulata*. All the syntypic material is extremely worn, only one specimen showing faint spiral sculpture.

The present material, while friable, shows good preservation of detail, and possesses the distinctive spiral lirae characteristic of *B. annulata*.

While only one of the specimens from the 50 m Complex shows the development of a shoulder on the upper whorl, approaching the condition in typical *B. annulata*, Barnard (1962) does note that some recent specimens show only a weak development of the shoulder. The present material removes any doubt that *B. magna* really is *B. annulata*.

The Hondeklip specimens occurred in a very fine sand, in a layer dominated by specimens of the bivalve *Dosinia sicarisinus* sp. nov., often with both valves in life position.

Distribution

Living *B. annulata* occurs from Saldanha Bay to Mozambique, from the low-tide mark, but more usually infratidally, to 100 m (Barnard 1958; Kilburn & Rippey 1982).

Fossil *B. annulata* has been recorded from Langebaan, Milnerton, Swartkops, Redhouse and Coega (Barnard 1959, 1962).

Nassarius cf. kochianus (Dunker, 1846)

Nassarius kochianus (Dunker), Kilburn & Rippey, 1982: 100, 213, pl. 23 (fig. 8).

Nassa kochiana: Barnard, 1959: 104, figs 22b, 23b; 1962: 189.

Material

SAM-PQ-KN546, 3 specimens, 10,9 × 6,1 mm, 9,1 × 5,1 mm, 7,6 × 4,1 mm, Koingnaas KL south face.

Previous records

Living: False Bay to Transkei, intertidal to shallow infratidal.

Fossil: Algoa Bay.

Remarks

With slightly fewer axial ribs (13–14 per whorl) than is usual for *N. kochianus* (15–18), the present material, however, does have only a single columella nodule, and in profile more closely resembles this species than it does *N. signatus* (Dunker, 1847). More specimens are needed to decide the range of variation in the number of axial ribs, before a more definite identification can be attempted.

Family Fasciolariidae

Fasciolaria dinglei sp. nov.

Figs 27, 28

Fasciolaria sp. Carrington & Kensley, 1969: 193, pl. 18 (?partim).*Material*

Holotype. SAM-PQ-AV547, 101 × 41 mm (apex and upper whorls eroded), Avontuur A, 50 m Complex.

Paratypes. SAM-PQ-AV548, 3 body whorl fragments, 7 specimens, 39,4 × 19,8 mm to 83,4 × 40,3 mm, Avontuur A, 50 m Complex.

Description

Shell with aperture longer than spire. Four to five postnatal whorls. Profile of whorls evenly convex. Third whorl with 12–13 fine spiral lirae; fourth with 15–16 lirae; body whorl with 50–55 lirae running on to anterior canal; lirae on upper



Fig. 27. *Fasciolaria dinglei*. Holotype. Scale = 10 mm.

body whorl near suture having finer intermediates appearing; lirae on base of body whorl becoming coarser and broader. Columella with 3 pleats, sometimes obscured in large specimens; low ridge on upper columella just below suture. Anterior canal about half length of rest of aperture, flexed to left. Inner surface of outer lip with up to 25 rounded ridges.

Remarks

Of the two specimens of *Fasciolaria* figured by Carrington & Kensley (1969, pl. 18c), the smaller may well be the present species. The larger, however, is undoubtedly a large *Burnupena*, lacking as it does an elongate anterior canal.

Carrington & Kensley (1969) noted the similarity of their specimen to *Fasciolaria lugubris* (Reeve, 1847). This similarity in overall proportions and general sculpture is again noted, but several differences easily separate the two species. The most distinctive feature of the new species is the presence of three pleats on the columella (*F. lugubris* is unpleated). The spiral sculpture of *F. dinglei* is much finer and the lines more numerous (up to 55 on the body whorl) than in *F. lugubris* (up to 30 on body whorl, and more raised).

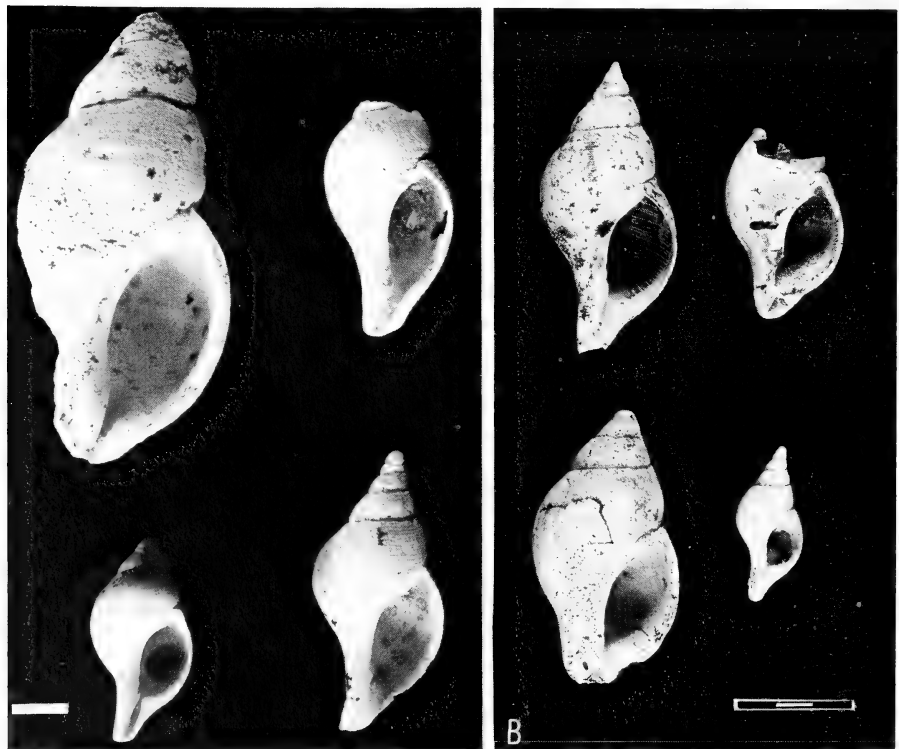


Fig. 28. *Fasciolaria dinglei*. A. Range of paratypes. Scale = 10 mm. B. Range of paratypes. Scale = 30 mm.

Etymology

The species is named for Professor Richard V. Dingle, Department of Geology, University of Cape Town.

Family **Olividae***Melapium hawthornei* sp. nov.

Fig. 29

Material

Holotype. SAM-PQ-KN549, 27,5 × 24,0 mm, Koingnaas KN-1.

Paratypes. SAM-PQ-KN550, 12 specimens, 23,4 × 16,7 mm to 26,1 × 20,1 mm, Koingnaas KN-1, 50 m Complex. USNM 400988, 4 specimens, 23,4 × 17,1 mm to 27,0 × 18,9 mm, Koingnaas KN-1, 50 m Complex.

Non-type material. SAM-PQ-KN551, 9 specimens, all worn and damaged, Koingnaas KL south face. SAM-PQ-KN366, 16 specimens, all damaged, Koingnaas KN-1, 50 m Complex.

Description

Shell 1,2 times longer than wide, of 4 postnatal whorls. Spire somewhat sunken, but still protruding. Body whorl globose, profile evenly convex, with very faint, shallow, spiral lines, and irregular axial growth lines. Parietal callus extending from body-whorl suture in evenly convex line to lower columella. Posterior canal short, but with distinct notch; anterior canal flexed to left; lower columella narrowed, with fasciole strong but barely visible in apertural view; outer lip evenly convex to notch at anterior canal.

Remarks

Two living and one fossil species of *Melapium* have been recorded from southern Africa, all of which differ from the present species.

Melapium lineatum (Lamarck, 1822), known from Still Bay to Zululand in depths of 30–160 m, is of comparable size to *M. hawthornei*, but possesses a more elevated spire; also, the lower columella is broader, with the fasciole being strong and visible in apertural view. *Melapium lineatum* also has a distinct concavity just above the fasciole origin, and below the bulge of the body whorl; *M. hawthornei*, by contrast, is evenly convex in this region.

Melapium elatum (Schubert & Wagner, 1829), from deeper water off Natal and Mozambique, has a much larger shell, with the lower columella very broad and with a very strong fasciole, and a distinct shoulder on the upper body whorl.

Melapium patersonae Bullen Newton, 1913, from the Neogene of Bredasdorp to Alexandria, Cape Province, is also a large shell, up to 70 mm in length, has a sunken spire, a well-developed posterior canal with the outer lip reaching posteriorly above the spire, and a very broad columella with a very strong carinate fasciole.

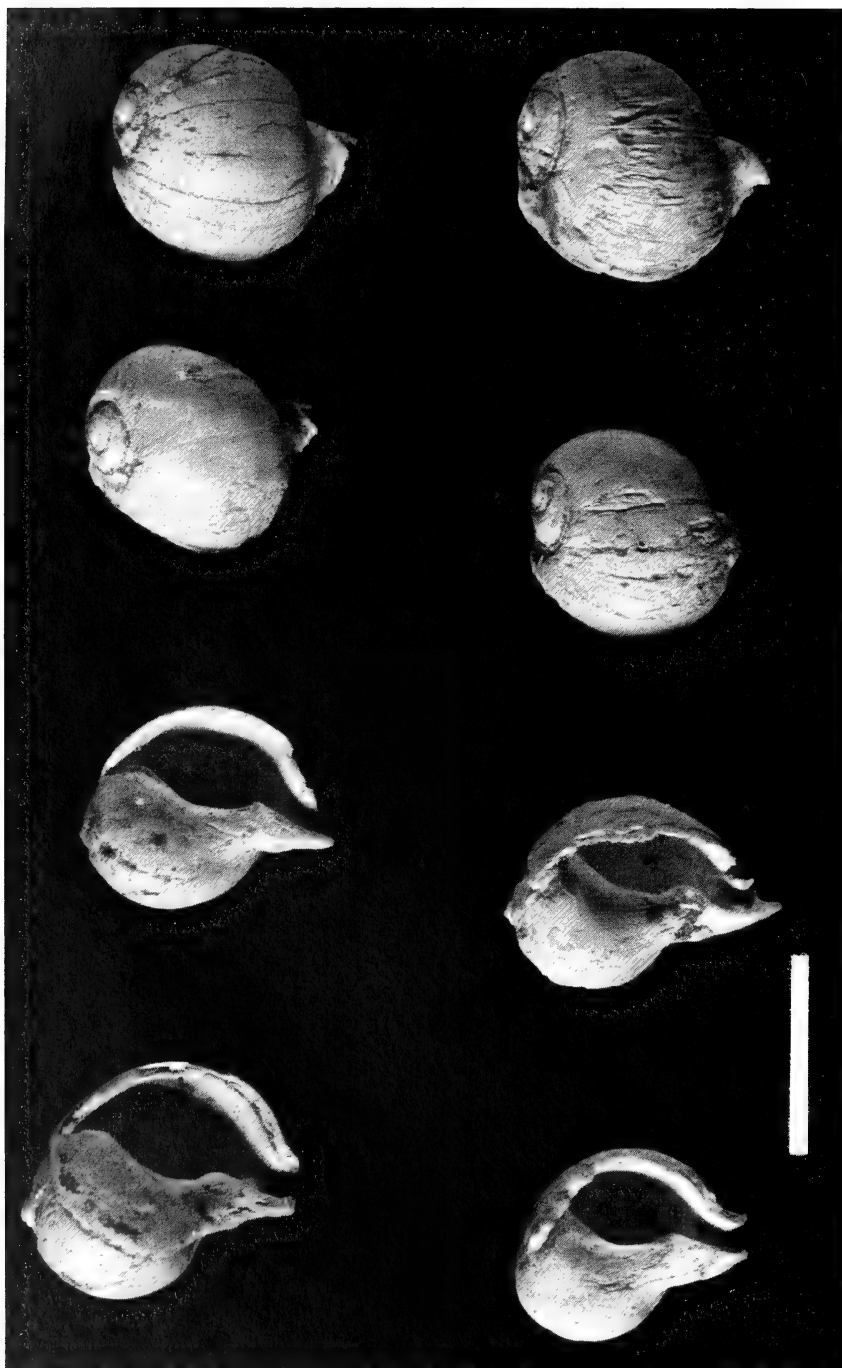


Fig. 29. *Melapium hawthornei*. Holotype at upper left corner, remainder of specimens paratypes. Scale = 20 mm.

Etymology

The species is named for Mr J. B. Hawthorne of De Beers Consolidated Diamond Mines.

Pseudoliva lutulenta sp. nov.

Fig. 30

Material

Holotype. SAM-PQ-KN552, 31,6 × 22,7 mm, Koingnaas KN-1.

Paratypes. SAM-PQ-KN553, 8 complete specimens, 20,7 × 15,8 mm to 29,2 × 21,2 mm, Koingnaas KN-1. USNM 400989, 3 complete specimens, 23,1 × 18,1 mm to 28,3 × 21,5 mm, Koingnaas KN-1.

Non-type material. SAM-PQ-KN373, 13 specimens (damaged), Koingnaas KN-1.

Description

Shell globose, thick-walled, longer than wide, of 4 whorls. Spire short. Whorl profiles evenly convex; suture somewhat incised. Columella callus smooth, convex, reaching posteriorly to level of suture, outline evenly convex on inner-lip body whorl; parietal node somewhat elongate, forming shallow groove-like posterior canal. Base with strong furrow running from shallow sinus in anterior outer lip, around lower body whorl, to midpoint of columella callus; second, less clearly defined groove anterior to strong groove, neither groove marked on inner surface of outer lip.

Remarks

Three major differences separate the present material from the apparently very similar living *Pseudoliva crassa* (Gmelin), known only from Angola, and figured and described as *P. plumbea* (Chemnitz) by Nicklés (1950: 107, fig. 189). The living species possesses two strong well-defined grooves on the anterior body whorl, the upper of which is marked by a narrow 'excroissance' on the internal surface of the outer lip. In the present species there is one strong groove and a far less well-defined more anterior groove. Neither groove is reflected by any structure on the internal surface of the outer lip. The columella callus in *P. crassa* is concave, and posteriorly narrowed to the posterior canal. In *P. lutulenta* the columella callus is convex, and posteriorly broadly rounded.

Böhm (1926) described two species of *Pseudoliva* from the Cretaceous of Bogenfels, South West Africa-Namibia, neither of which bears much resemblance to the present species. *Pseudoliva thielei* Böhm shows enormous columella callus development, and has several spiral ridges on the shell base; *P. leutweini* Böhm is a much larger species than *P. lutulenta*, with a massive upper columella callus.

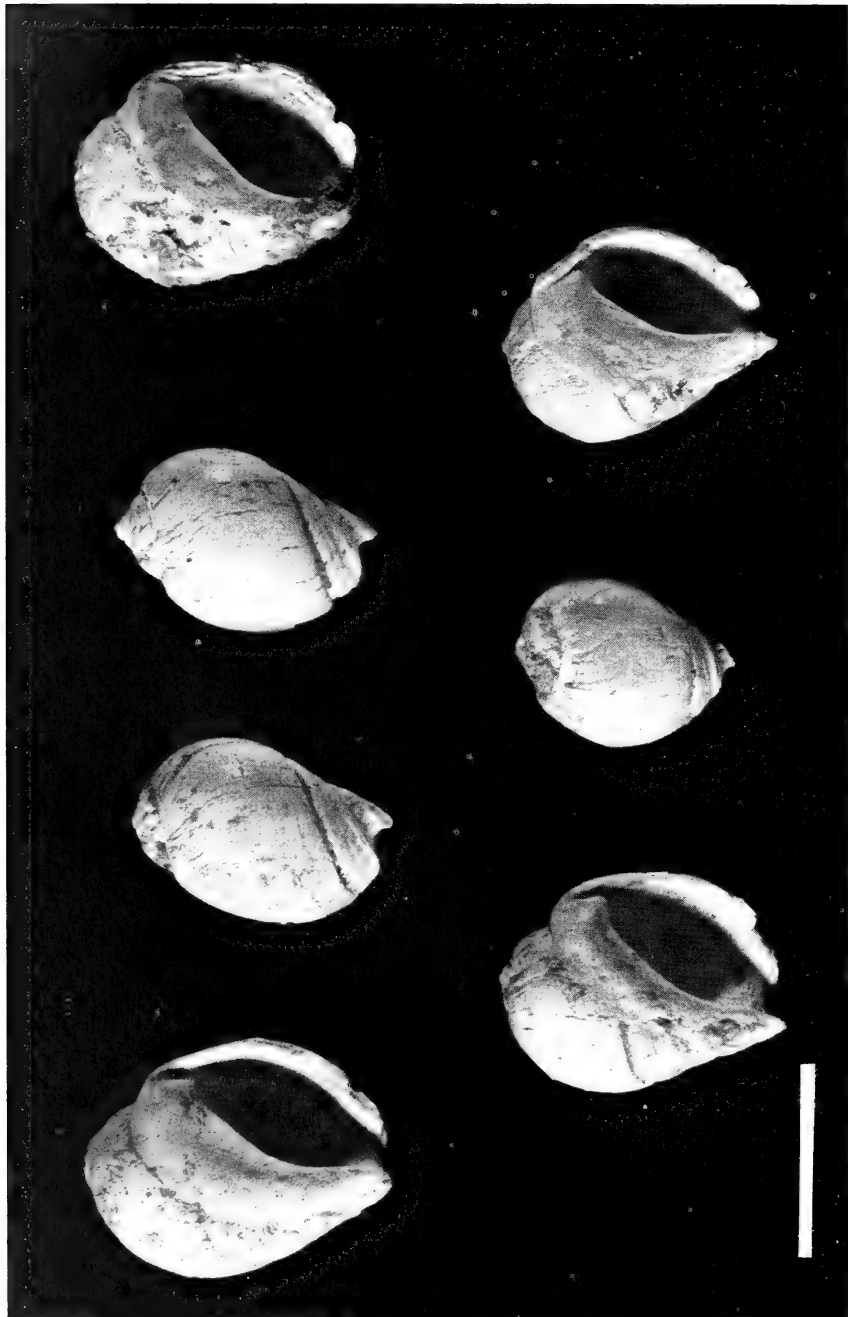


Fig. 30. *Pseudoliva lutulenta*. Holotype at upper left corner, remainder of specimens paratypes. Scale = 20 mm.

Etymology

The specific name is derived from the Latin 'lutulentus', covered with mud, and alludes to the fine sediments in which the species was found.

Family Turridae

Drillia tempestae sp. nov.

Fig. 31

Material

Holotype. SAM-PQ-HB554, 12,1 × 5,1 mm, Hondeklip Zone 3, 50 m Complex.

Paratypes. SAM-PQ-HB555, 10 specimens, 6,3 × 3,4 mm to 19,4 × 7,7 mm, Hondeklip Zone 3, 50 m Complex. USNM 400990, 10 specimens, 6,3 × 2,0 mm to 16,4 × 7,2 mm, Hondeklip Zone 3, 50 m Complex.

Non-type material. SAM-PQ-SL260, 1 specimen, 19,9 × 8,4 mm, Swart-lintjies River, spoil heap. SAM-PQ-HB556, approx. 50 specimens, Hondeklip Zone 3, 50 m Complex.

Description

Protoconch of 1½ smooth whorls; 6½–7 postnatal whorls. Spire 1,3–1,5 times length of aperture. Sculpture consisting of rounded axial ribs and fine spiral lirae; axial ribs slightly oblique, occasionally perpendicular, rounded, with distinct shoulder well below upper suture line, reaching lower suture. Postnatal whorl 3 with 9 axial ribs, 6–9 spiral lirae; ribs increasing to 11 on body whorl, lirae to 10–18 on penultimate whorl; outer lip with 20–24 spiral lirae running on to outer surface of siphonal canal. Lirae equal in width on spire, becoming broader on body whorl and siphonal canal. Anal sinus in outer lip shallow. Columella callus smooth; anterior siphonal canal short, well marked.

Remarks

The present species resembles *Drillia caffra* (Smith, 1882) in overall proportions, but differs in details. The earlier species has more axial ribs per whorl (11–12 on early whorls, 15–18 on later whorls), more spiral lirae (6 on early whorls, up to 30 on last whorl), and possesses a deep anal sinus.

As generic placement in the Turridae is so dependent on radula structure, the present material is placed in *Drillia* purely because of an overall resemblance to some species in that genus.

Etymology

The specific name, from the Latin for 'of a storm', alludes to the storm conditions that probably caused some of the Hondeklip fossil accumulations.

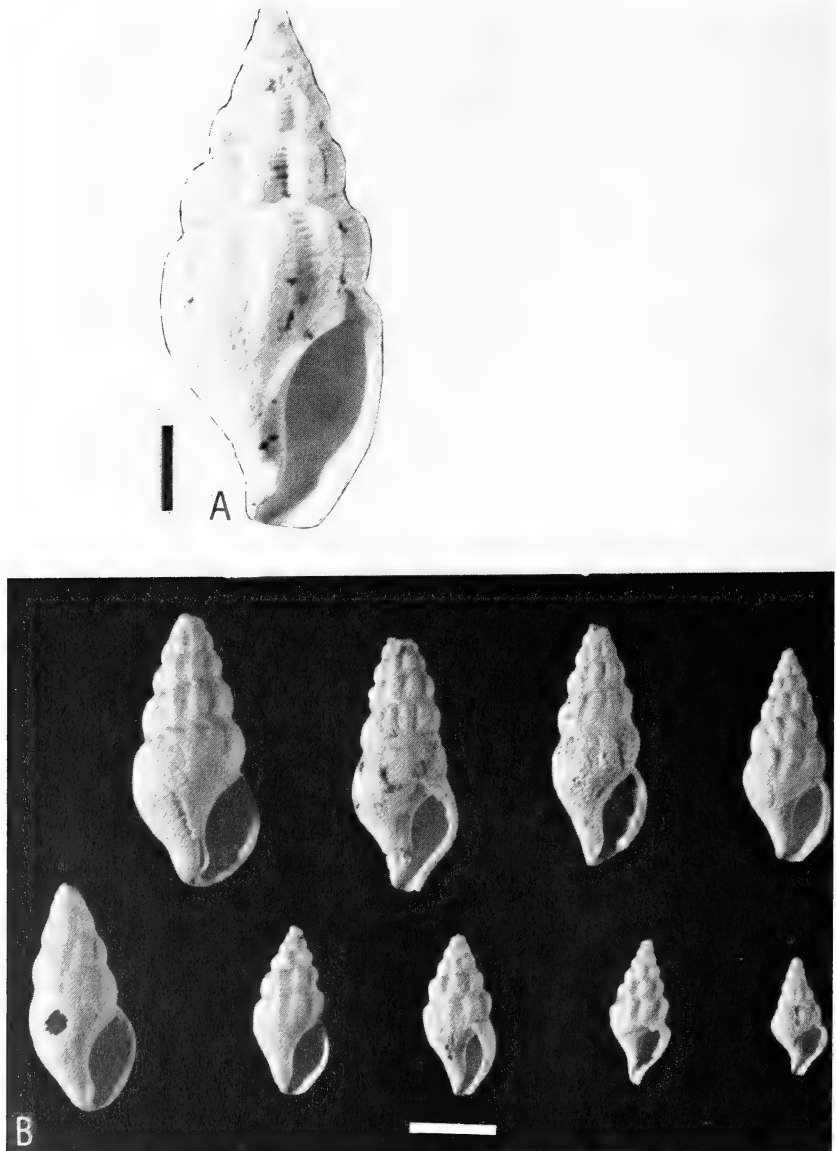


Fig. 31. *Drillia tempestae*. A. Holotype. Scale = 2 mm. B. Range of paratypes. Scale = 5 mm.

Family Terebridae

Terebra canisaxi sp. nov.

Fig. 32

Material

Holotype. SAM-PQ-HB557, $21,4 \times 6,5$ mm, Hondeklip Zone 12, 50 m Complex.

Paratypes. SAM-PQ-HB558, 10 specimens, $15,2 \times 4,9$ mm to $23,1 \times 6,9$ mm, Hondeklip Zone 12, 50 m Complex. USNM 400991, 10 specimens, $15,7 \times 5,6$ mm to $23,1 \times 6,4$ mm, Hondeklip Zone 12, 50 m Complex.

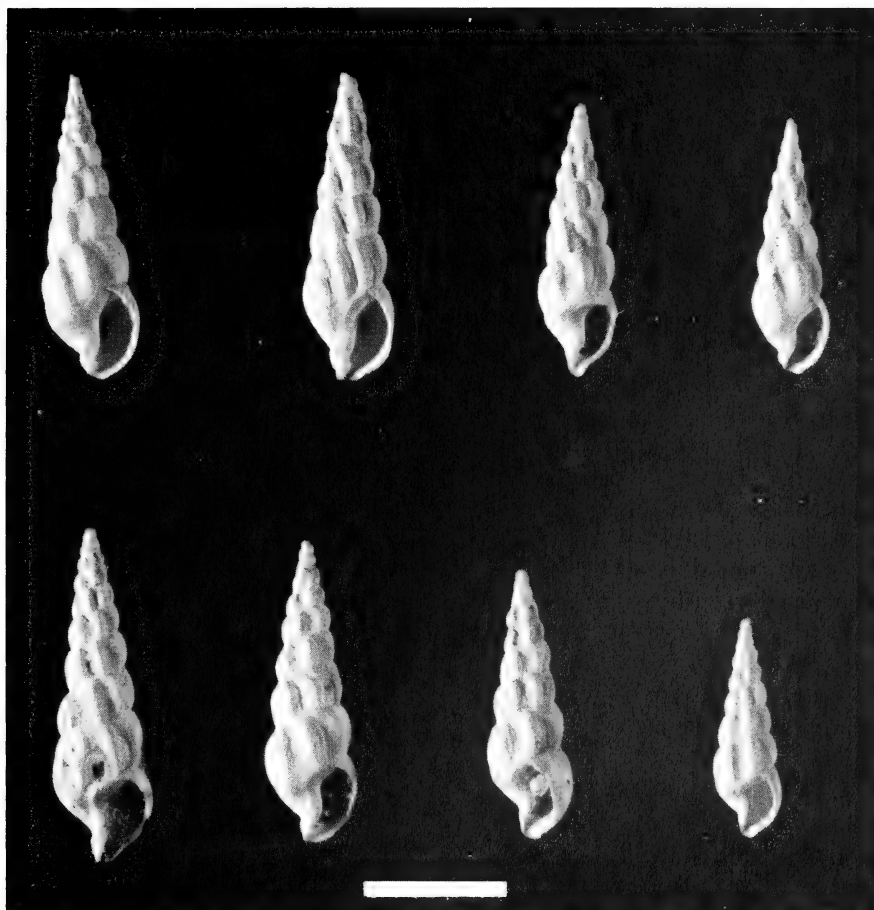


Fig. 32. *Terebra canisaxi*. Holotype at upper left corner, remainder of specimens paratypes. Scale = 10 mm.

Non-type material. SAM-PQ-HB559, 4 specimens, $14,6 \times 4,9$ mm to $17,7 \times 5,7$ mm, many fragments, Hondeklip Zone 12, 50 m Complex. SAM-PQ-HB331, 30 specimens, Hondeklip Zone 12, 50 m Complex.

Description

Shell of protoconch of $2\frac{1}{2}$ smooth whorls, plus 7 postnatal whorls. Postnatal whorl sculpture consisting of strong, rounded, axial ribs running from upper to lower suture, sometimes alternating from one whorl to next, sometimes continuous. Postnatal whorl 1 with 9 ribs, following 6 whorls each with 8–9 ribs, body whorl with 9–10 ribs. Anterior canal short, open, flexed to left. Base rounded. Columella lacking pleats, smooth; low fasciole present. Spiral groove absent.

Remarks

This species closely resembles *Terebra lightfooti* Smith, 1903, recorded alive from Saldanha Bay to the Agulhas Bank to a depth of 62 m. Barnard (1969: 596) described this species as having eight postnatal whorls. *Terebra lightfooti* is a marginally more slender species than *T. canisaxi*, with slightly more numerous axial ribs (11–12 on last three whorls, as against 8–9 in *T. canisaxi*).

Etymology

The specific name is the Latinized form of 'dog stone', a direct translation of the name of the type-locality, Hondeklip.

Class BIVALVIA

Family Glycymeridae

Glycymeris fulleri sp. nov.

Figs 33, 34

Material

Holotype. SAM-PQ-SL561, both valves, $58,0 \times 61,5$ mm, Swartlintjies SL-20, 50 m Complex.

Paratypes. SAM-PQ-SL562, both valves, $38,0 \times 40,5$ mm, Swartlintjies SL-20, 50 m Complex. SAM-PQ-KN560, right valve, $40,2 \times 44,1$ mm, Koingnaas KN-1, 50 m Complex. SAM-PQ-KN563, 3 left valves, $25,0 \times 26,8$ mm, $36,2 \times 40,0$ mm, $46,3 \times 46,0$ mm (distorted), 1 right valve, $37,1 \times ?$ mm, Koingnaas KN-1, 50 m Complex. USNM 400992, 2 left valves, $23,6 \times 24,9$ mm, $42,9 \times ?$ mm, 1 right valve, $34,8 \times ?$ mm, Koingnaas KN-1, 50 m Complex.

Description

All material in poor condition, with external surfaces exfoliating, and shape frequently deformed. Shell slightly inequilateral, posterior margin slightly more pointed than anterior margin; slightly wider than high. Sculpture of about 40 radiating, apparently flattened ribs, becoming obsolete in anterior and

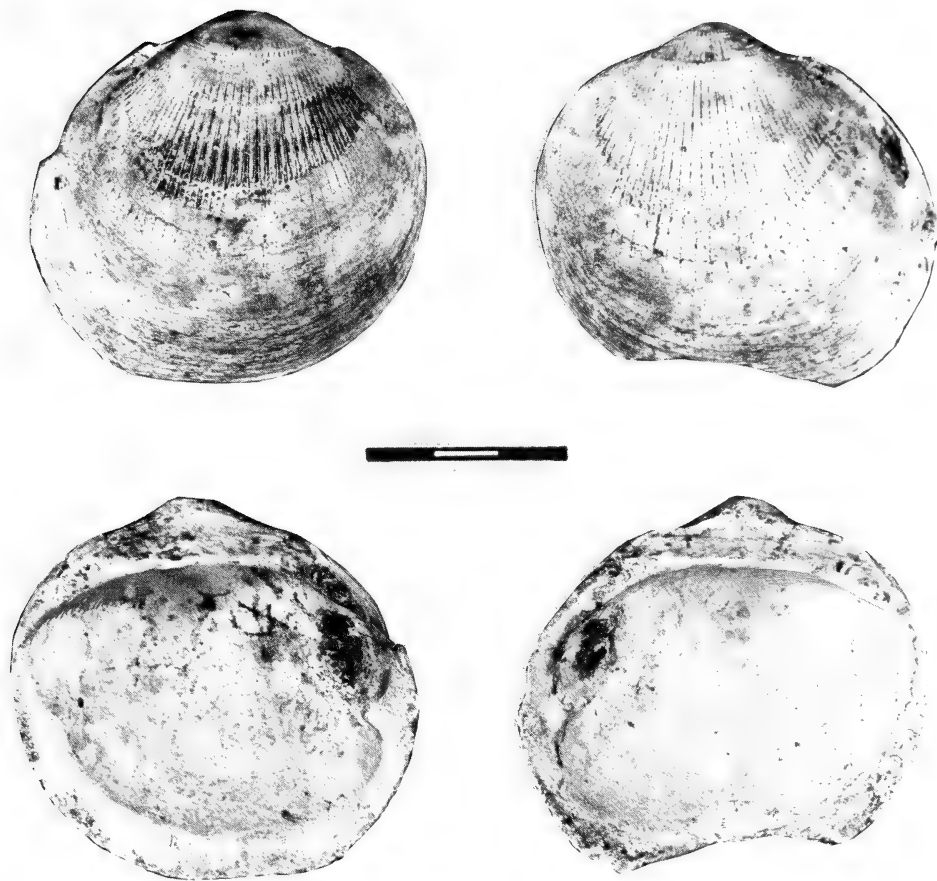


Fig. 33. *Glycymeris fulleri*. Holotype, external and internal views of both valves.
Scale = 30 mm.

posterior part of shell. Ventral margin faintly crenulate in external view, internally more strongly crenulate. Anterior and posterior adductor muscle scars situated on faint ledge. Hinge area with teeth discontinuous below umbo, divided into two groups, each of 7–9 teeth.

Remarks

Glycymeris fulleri resembles the living southern African east-coast species *G. queketti* (Sowerby, 1897) in having the muscle scars situated on faint ledges, but is a smaller and more inequilateral species. Barnard (1962: 183) mentions two specimens referred to *G. queketti* from Skulpfontein Point, Hondeklipbaai area, by Krige (1927), but questioned the identification.

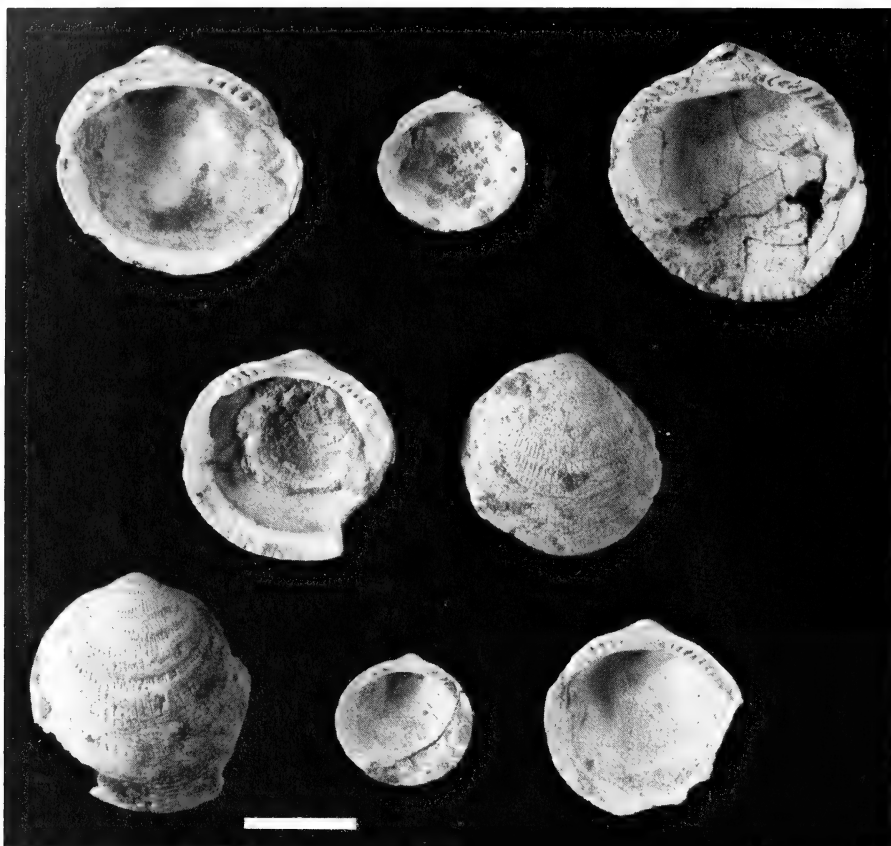


Fig. 34. *Glycymeris fulleri*. Range of paratypes. Scale = 20 mm.

Glycymeris connollyi Tomlin, 1923, known living from Table Bay to Natal, is smaller than the present species, and more trigonal in outline.

Glycymeris borgesii (Cox, 1946) (= *G. africana* Cox, 1939), known from the Neogene of Ysterplaat, Cape Province (Tankard 1975a) as well as from the Alexandria Formation in the Port Elizabeth area, is a much larger species (up to 100 mm diameter), with the hinge teeth in a continuous band.

Glycymeris ovata (Broderip), recorded from the Pliocene and Pleistocene of Chile by Herm (1969) also shows the tooth row of the hinge divided into two parts, but this species is less markedly inequilateral and somewhat more trigonal than the present species.

Etymology

The species is named for Professor A. O. Fuller, Department of Geology, University of Cape Town.

Family **Ostreidae**
Ostrea cf. subradiosa Böhm

Fig. 35

Ostrea digitilina, non Dubois, Böhm & Weisfermel, 1913: 61, fig. 1a, pl. 8 (fig. 2).
Ostrea subradiosa Böhm, 1926: 56, text table A (figs 1–3).

Material

SAM-PQ-AV571, one left valve, 93 × 83 mm, Avontuur A, 50 m Complex.

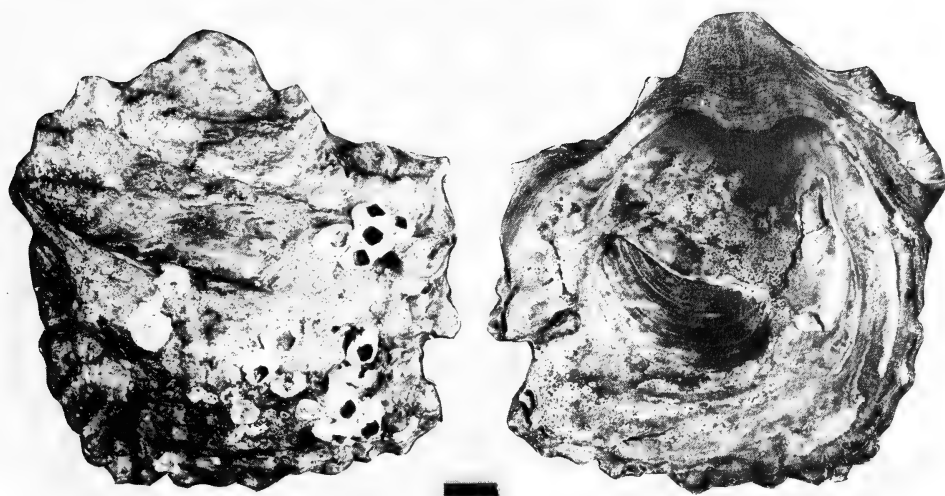


Fig. 35. *Ostrea cf. subradiosa*. External and internal view of left valve. Scale = 10 mm.

Remarks

The present specimen has been compared with material in the South African Museum (SAM-K4936) from Bogenfels, as well as with the original descriptions and figures. Neither of the figures of Böhm & Weisfermel (1913) shows a row of pits in the shell margin close to the hinge area. The figure of Böhm (1926), however, shows such a row of pits. The present specimen, while having the strong radiating external ribs seen in *O. subradiosa*, lacks these marginal pits. A more definite identification on the basis of a single specimen is not possible.

Family **Isognomonidae*****Isognomon gariesensis* sp. nov.**

Fig. 36A

Material

Holotype. SAM-PQ-HB564, incomplete right valve, upper (dorsal) part of valve missing, greatest length 158 mm, greatest width (across hinge area) 90,9 mm, Hondeklip A Block, 50 m Complex.

Paratypes. SAM-PQ-HB263, 1 incomplete left valve, Hondeklip A Block, 50 m Complex. SAM-PQ-KN565, 2 incomplete left valves (one 145 mm in length), Koingnaas KL south face.

Non-type material. SAM-PQ-KN368, numerous friable fragments, Koingnaas KN-1.

Description

Shell very thick (up to 40 mm on ventral margin), becoming thinner posterodorsally. Hinge with 11 elongate ligamental grooves; hinge width 36,5 mm.

Remarks

The genus *Isognomon* is largely a warm-water form. On the west African coast, living *Isognomon* occurs as far south as the Congo (Nicklés 1950: 172). On the east African coast, *I. anomioides* (Reeve, 1858) commonly occurs in rock pools as far south as the Transkei coast. *Isognomon perna* occurs occasionally in Natal. Both these latter species reach a total length of about 66 mm and are thin-shelled.

Isognomon cf. *gaudichaudi* (d'Orbigny, 1842) (from the Miocene of Chile) was recorded from Needs Camp, Cape Province (Woods 1908; Newton 1913) and originally was thought to be of Cretaceous age, but later was referred to the Cenozoic. The species has also been recorded from Redhouse, Koega, and Bushmans River, Cape Province. The specimens examined in the South African Museum are from Redhouse and Swartkops (Fig. 36B). Newton (1913) compared the Cape Province specimens with *I. maxillata* (Lamarck, 1801) from Europe, *I. conradi* (d'Orbigny, 1842) from Virginia, U.S.A., and *I. gaudichaudi* (d'Orbigny) from Chile, and on the basis of the hinge similarities decided that the South African specimens most closely resembled the South American species.

The present west-coast material is similar to the material from the Eastern Province in hinge structure, but is much thicker and heavier. The ventral marginal sinuosity of the *Isognomon* cf. *gaudichaudi* is more marked than in the Hondeklip material. While it is unlikely that either the present samples or the Eastern Province material is conspecific with the Chilean species, there is precedent for this distribution pattern. Kensley & Penrith (1970) recorded three species of mytilid bivalve molluscs, and one brachiopod species from northern South West

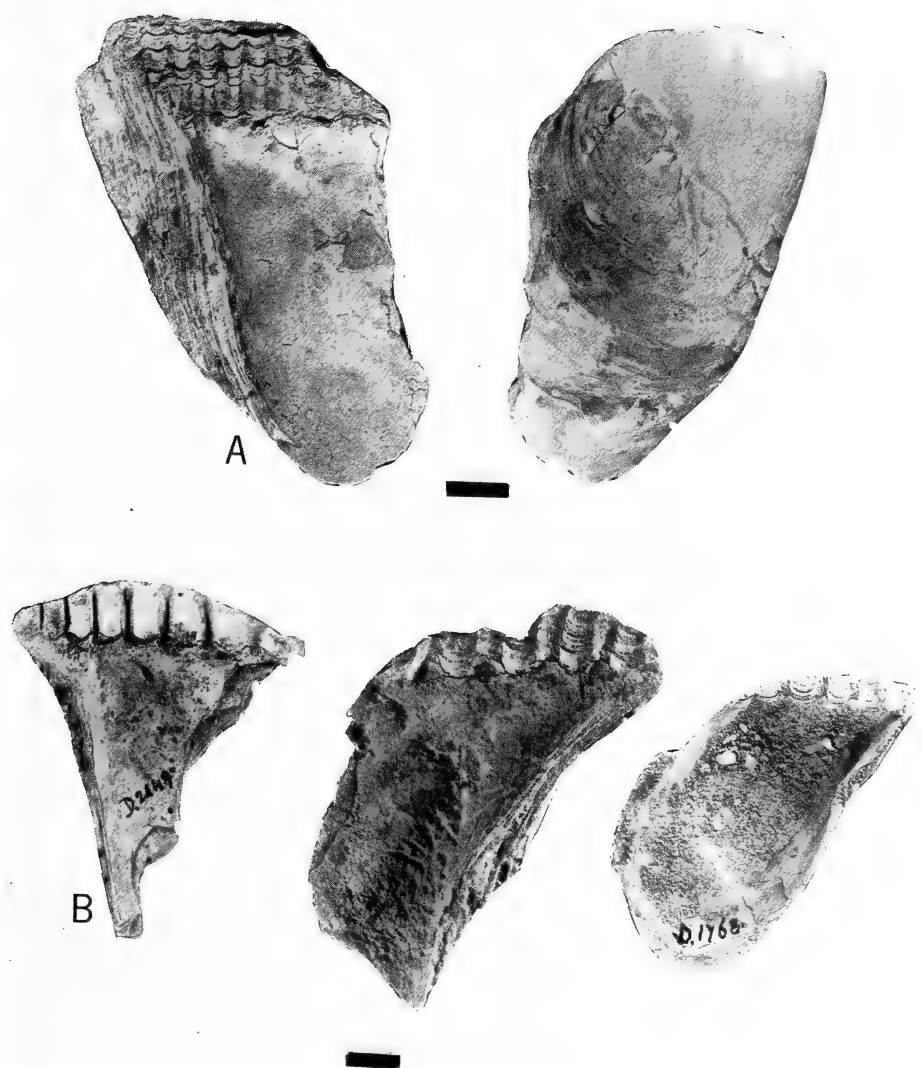


Fig. 36. A. *Isognomon gariesensis*. Holotype. B. *Isognomon 'gaudichaudi'*. Three specimens from Redhouse, Cape Province. Scales = 10 mm.

Africa–Namibia and Angola that occur in Pacific South America, while Kensley (1985*b*) recorded the South American thaidid *Concholepas* as a fossil from the west coast of South Africa. Until more complete material is available, it is wiser to give the present material new specific status, rather than confuse it with earlier-described species.

Etymology

The specific name is derived from Garies, the district in which the Hondeklip and Koingnaas localities are found.

Family **Carditidae**

Cardita unica sp. nov.

Fig. 37

Material

Holotype. SAM–PQ–KN566, 1 right valve, 44,0 × 67,5 mm, Koingnaas KL south face.

Description

Shell robust, thick, oblong, anterior margin rounded, ventral margin flattened, posterior margin more pointed than anterior. External sculpture consisting of 27 radiating ribs, becoming broadly flattened near ventral margin, separated by narrow grooves; ribs on posterior part of shell narrower than on rest of shell. Concentric growth lines irregular, wavy. Lower anterior and posterior margin and ventral margin on shell interior crenulate, crenulations largest at posteroventral corner. Anterior adductor scar oval; small circular hollow dorsal to anterior muscle scar, hidden under anterior hinge line. Posterior adductor scar anteriorly truncate, posteriorly rounded. Hinge line broad, solid; anterior lateral tooth almost vertical, short, separated from anterior cardinal tooth by triangular pit; anterior cardinal tooth acutely triangular with posterior margin twice length of anterior margin, separated from posterior cardinal tooth by narrowly triangular oblique groove; posterior cardinal tooth elongate, with horizontal dorsal part and oblique ventral part. Ventral margin of hinge area sinuous.

Remarks

The present specimen bears no resemblance to any carditid, fossil or living, recorded from southern or west Africa.

Etymology

The specific name, derived from the Latin 'unicus', meaning unique, refers to the fact that only a single valve of this species has been found, and that it bears no resemblance to any African carditid.



Fig. 37. *Cardita unica*. Holotype, external and internal view of right valve. Scale = 10 mm.

Cuna aquaedulcensis Kensley, 1977

Fig. 38

Cuna aquaedulcensis Kensley, 1977: 203, fig. 15.

Material

SAM-PQ-HB567, about 50 valves, largest specimen $7,5 \times 7,1$ mm, Hondeklip, 30 m Complex.

Description

Right valve, hinge with elongate anterior cardinal tooth, median tooth narrowly triangular, separated from anterior tooth by narrow triangular gutter.



Fig. 38. *Cuna aquaedulcensis*. Hinge details of left (upper) and right (lower) valves.

Posterior cardinal tooth reduced to short low rounded ridge. Left valve, hinge with elongate rounded ridge on anterior margin, running from anterior adductor muscle scar to umbo; 2 median teeth, anteriormost larger, smaller tooth narrow and lower; posterior tooth separated from margin by relatively deep groove.

Previous records

Quartzose Sand Member, Langebaanweg, Pliocene.

Remarks

As only two right valves were available when the species was described, it was thought useful to supplement the description, now that far more material is available.

Family **Veneridae**

Dosinia (Dosinia) sicarisinus sp. nov.

Figs 39, 40

Material

Holotype. SAM-K4877, both valves, 75,7 × 72,4 mm, thickness of two valves together 27,1 mm, Somnaas SN4, Hondeklip, 50 m Complex, coll. A. J. Tankard.

Paratypes. SAM-PQ-HB568, 4 left valves, 66,7 × 65,5 mm, 63,1 × 65,0 mm, 57,4 × 57,7 mm, ? × 66,9 mm, 1 right valve, 67,4 × 70,7 mm, Hondeklip

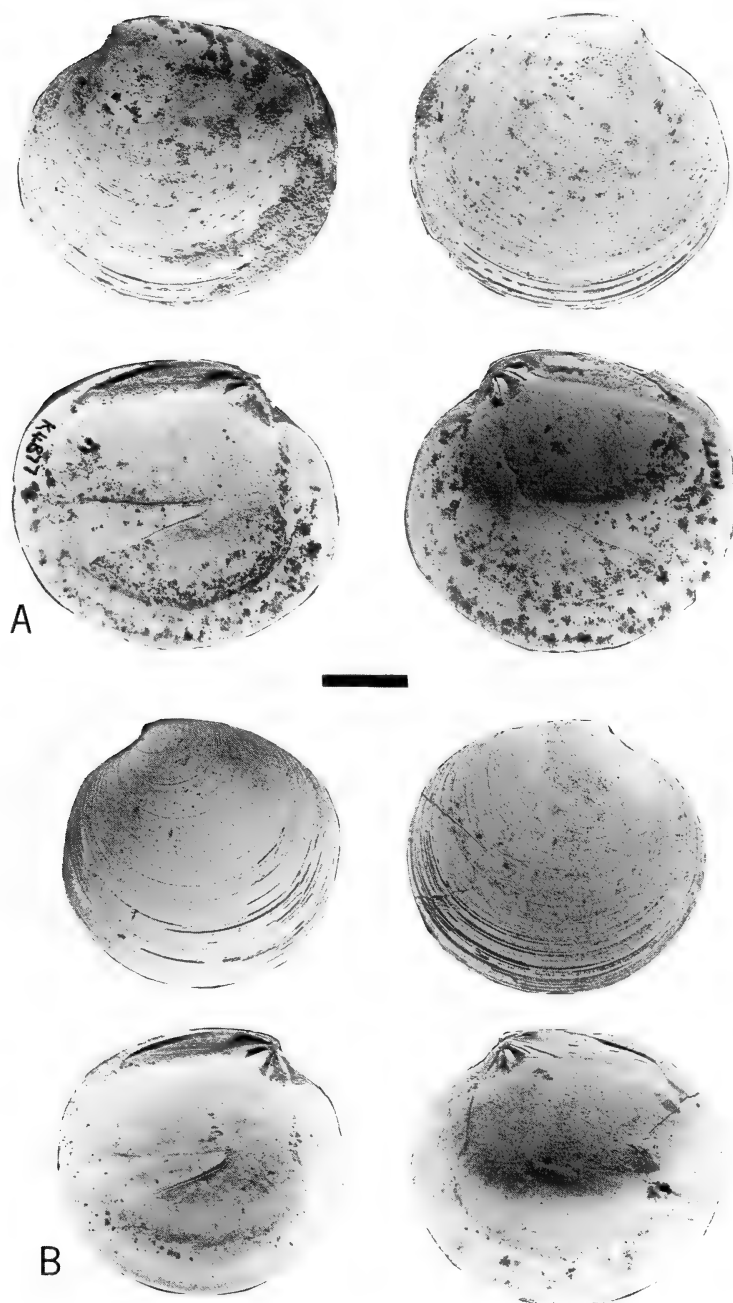


Fig. 39. *Dosinia sicarisinus*. A. Holotype, external and internal view of both valves. B. Paratype. Scale = 20 mm.



Fig. 40. *Dosinia sicarisinus*. Hinge details of right (upper) and left (lower) valves.

Zone 12, 50 m Complex. SAM-PQ-HB569, both valves (hinge of right valve missing), $62,8 \times 68,0$ mm, Hondeklip Zone 4A, 50 m Complex. USNM 400993, both valves, $63,6 \times 62,5$ mm, 2 left valves, $66,3 \times 64,5$ mm, $61,8 \times 63,2$ mm, Hondeklip, 50 m Complex.

Description

Shell proportions somewhat variable, generally longer than wide but occasionally wider than long. Sculpture of concentric lines, barely lamellose anteriorly and posteriorly. Lunule well defined; escutcheon lacking. Pallial sinus horizontal to slightly ascending, apically narrowed. Left and right hinges with small anterior lateral tooth set at angle to anterior cardinal tooth; posterior cardinal tooth in right valve bifid; anterior cardinal tooth in left valve much less markedly bifid, with very narrow longitudinal slit.

Remarks

The present material bears little resemblance to the extant species of *Dosinia* from southern Africa. Apart from attaining a much larger size than any of the living species, *D. sicarisinus* also differs in the very distinctive narrowly triangular pallial sinus that reaches to below the umbo. *Dosinia exoleta* (Linnaeus) of the Mediterranean, and also known from Norway to North Africa, has a broader pallial sinus, and possesses lamellar concentric rings.

In general appearance and size, the present material resembles some of the Tertiary species from New Zealand, especially *D. (Raina) bartrami* Laws, 1930. This latter, however, has a shallow pallial sinus, and the shallow lunule of the subgenus (see Keen 1969: N679). *Dosinia sicarisinus* is placed in the subgenus *Dosinia* for lacking an escutcheon and lamellose concentric rings.

Etymology

The specific name is derived from the Latin 'sicarius', a murderer, and 'sinus', a bay, and alludes to Moordenaarsbaai, a coastal embayment close to the Hondeklip type localities.

Family **Pholadidae**

Barnea truncata (Say, 1822)

Barnea truncata: Nicklés, 1950: 232, fig. 454. Barnard, 1964: 565. Kilburn & Rippey, 1982: 203. Kensley, 1985a: 116.

Material

SAM-PQ-KN356, 2 specimens, left and right valves, approx. 60 mm and 75 mm in length; right valve, approx. 50 mm in length, Koingnaas KN-1. SAM-PQ-HB26, 3 worn hinges, Hondeklip, 30 m Complex.

Previous records

Living: Senegal to Angola; east coast of U.S.A.; numerous fresh dead shells from Table Bay in South African Museum collection.

Fossil: Milnerton, Table Bay (Late Pleistocene); borehole in Kuiseb River, South West Africa-Namibia, 9 miles (14,5 km) from sea (Geological Survey, determined by K. H. Barnard).

Class SCAPHOPODA

Family **Dentaliidae**

Dentalium sp.

Fig. 41

Material

SAM-PQ-KN570, fragments, Koingnaas KN-1. SAM-PQ-KN376, several fragments, Koingnaas KN-1.

Description

Shell gently convex; with 16 rounded ribs at narrower end (1,8 mm diameter); ribs equal in width to concave furrows between them; at about 3,0 mm diameter, much narrower intermediate rounded ribs (1 between 2 larger ribs) becoming apparent; 26 ribs present.

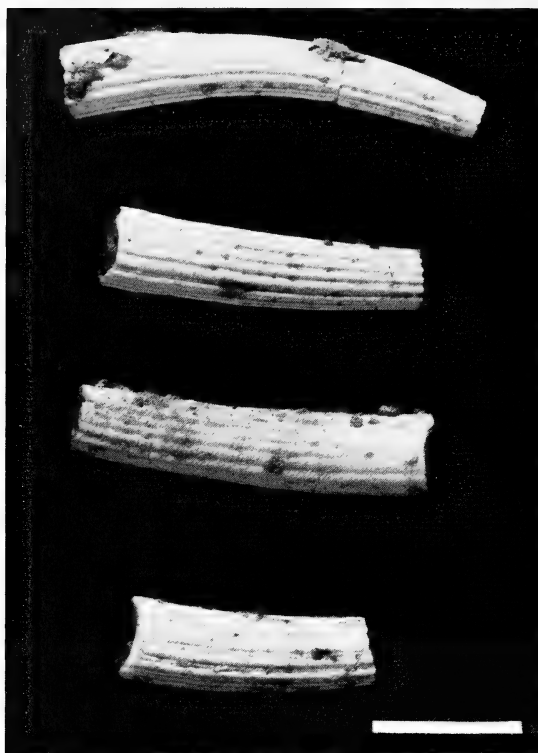


Fig. 41. *Dentalium* sp. Fragments. Scale = 5 mm.

Remarks

The present material bears little resemblance to any living species of *Dentalium* described from southern Africa.

DISCUSSION

FAUNAL COMPOSITION

The following table is a broad-scale analysis of the faunal composition of the fossil molluscs from the Hondeklip area collected during this study. Material identified to generic level only is excluded (15 genera).

Total number of species	92	
Total number of extinct species	45	(49%)
Lyellian percentage (percentage extant)		51%
Total number of species still living on east and west coasts	27	
Total number of species living on east coast only	11	
Total number of species with West African-Mediterranean affinities	9	

Extinct species also present in east-coast deposits	4	
Total number of species from 50 m Complex	78	
Total number of extinct species from 50 m Complex	37	(47%)
Lyellian percentage		53%
50 m Complex species recorded by Carrington & Kensley (1969) but not found during course of this study	4	
(of which 3 are extinct)		
Total number of species from 30 m Complex	48	
Total number of extinct species from 30 m Complex	19	(40%)
Lyellian percentage		60%
Number of species common to 50 m and 30 m Complexes	34	
Number of extinct species in common	11	

From the previous summary, several topics require further comment. Notably, the 50 m Complex shows a higher diversity than the 30 m Complex (78 species as against 48). A glance at the species list (Table 1), which records the depositional environment of the beds from which the molluscs were obtained, shows that a greater range of environments was available in the 50 m Complex (viz. back-barrier, tidal-inlet, and distal lower-shoreface deposits, as against only near-shore open-coast deposits in the 30 m Complex). It is thus tempting to attribute the higher diversity of the 50 m Complex to the wider range of habitats. However, exclusion of specimens obtained only from 50 m Complex tidal-inlet and back-barrier deposits from the species list removes only nine species (two extinct), and the comparative diversity becomes 69 species (35 extinct) as against 48 species (19 extinct). This reflects the fact that the shelly beds in the 50 m Complex back-barrier-related facies are transported assemblages consisting of a mixture of calm-water and open-coast forms. Additionally, calm-water species may also inhabit the substrate below average wave-base, and become incorporated into open-coast facies, provided the open-coast temperature regime is within species tolerances.

As shown for the Late Pleistocene at Verlorevlei (Tankard 1975), thermally anomalous back-barrier environments increase species-diversity by the addition of warm-water taxa to the faunal composition. A modern example of such localized habitats is Sandvis Lagoon (Sandwich Harbour) near Walvis Bay (Kensley & Penrith 1977). However, in such cases the contrast between the back-barrier and open-coast assemblages is clear-cut. This is evidently not the case with the Hondeklip fauna, but this observation is qualified by the absence of large life assemblages preserved in the 50 m Complex back-barrier facies.

In the 50 m Complex back-barrier facies, only *Dosinia sicarisinus*, *Donax haughtoni*, *Phaxas decipiens*, *Standella namaquensis*, and *Tivela* cf. *compressa* have been found in life positions. In open-coast facies, *Lutraria* sp. has been found in life position around the lower-shoreface-upper-shoreface facies boundary in the 50 m Complex; in the 30 m Complex, *Donax rogersi* and *Standella*

namaquensis occur in life positions in the upper shoreface. *Striostrea margariticea* has been found attached to rocks in open-coast contexts in both complexes.

In Table 1 the species obtained from deposits on the properties of Koingnaas and Swartlintjiesrivier have been indicated separately owing to the unique additions to the faunal list those beds have contributed. In the case of Koingnaas (KN) and Swartlintjiesrivier (SL) samples, this is further warranted since the beds are distal lower-shoreface deposits of the 50 m Complex. The curious mix of intertidal and deeper-dwelling forms (e.g. *Dentalium*, *Ringicula*, *Tugali*, and *Turritella declivis*) in these samples, together with the muddy nature of the enclosing sediment, is consistent with a depositional environment transitional to offshore conditions. As such, the KN sample has contributed most to environmentally-based diversity in the 50 m Complex.

Removing species unique to these samples (KN, SL, and KL) from the faunal list results in a 50 m–30 m Complex diversity contrast of 64 species (30 extinct) as against 39 species (14 extinct), respectively. Excluding these examples, as well as species from the 50 m Complex tidal-inlet and back-barrier facies from the faunal list, results in a diversity contrast of 54 species (28 extinct) as against 39 species (124 extinct) for the 50 m and 30 m Complexes, respectively. Only by not excluding the KL sample from the latter calculation is the diversity contrast narrowed: 54 species (50 m Complex) as against 48 (30 m Complex). Thus the higher diversity of the 50 m Complex is either real, or an



Fig. 42. Mactrid hinge remains from Koingnaas KL south face. Scale = 30 mm.

unavoidable bias due to the nature of the available exposures. In addition, any reworked forms possibly present in the 30 m Complex will reduce the diversity contrast.

TABLE 1

Species of Mollusca obtained from four properties in the Hondeklip area of the Namaqualand coast, reflecting the complex and depositional facies from which they were obtained.

Habitat: R = Rocky, S = Sandy, RiS = Rock in sand, M = Muddy. W/E: Species confined to either west (W) or east (E) coasts. TIL = Tidal-inlet facies. BBR = Back-barrier facies. USH = Upper-shoreface facies. LSH = Lower-shoreface facies. DLS = Distal lower-shoreface facies. KN = Koinaas KN. KL = Koinaas KL. SL = Swartlinterjies SL. † = Extinct.

Species	Habitat	W/E	50 m Complex					30 m Complex		
			TIL	BBR	USH	LSH	DLS (KN/SL)	USH	LSH	LSH (KL)
GASTROPODA										
<i>Afrocominella capensis</i> (Dunker in Philippi, 1844)	R		+	+	+					
<i>Amblychilepas scutellum</i> (Gmelin, 1791)	R		+	+	+			+		
† <i>Argobuccinum casus</i> sp. nov.				+	+		+			
† <i>Bolma anoropha</i> sp. nov.							+			
<i>Bullia annulata</i> (Lamarck, 1816) . .	S			+	+					
<i>Bullia digitalis</i> (Dillwyn, 1817) . .	S		+	+	+			+		+
<i>Bullia laevis</i> (Gmelin, 1791)	S/M		+							
† <i>Burnupena aestus</i> sp. nov.				+	+					
<i>Burnupena papyracea</i> (Bruguère, 1789)	R		+	+	+					
† <i>Burnupena rogersi</i> sp. nov.			+							
† <i>Calliostoma depressa</i> Carrington & Kensley, 1969				+						
<i>Cantharidus (Jujubinus) striatus</i> . . (Linnaeus, 1758)		W		+						
<i>Calyptraea helicoidea</i> Sowerby, 1883	R	E								+
† <i>Calyptraea kilburni</i> nom. nov.	?R		+	+	+		+	+	+	+
† <i>Calyptraea viridarena</i> Carrington & Kensley, 1969	?R			+	+					
† <i>Clanculus lutosus</i> sp. nov.							+			
† <i>Clanculus murrayi</i> Carrington & Kensley, 1969			+	+	+				+	
<i>Conus mozambicus</i> Hwass in Bruguère, 1789	R		+	+	+			+		
<i>Crepidula porcellana</i> Lamarck, 1801	R	W		+			+			
† <i>Crepidula deprima</i> sp. nov.	R		+	+	+					
<i>Cylichna tubulosa</i> Gould, 1859 . .		E					+			
<i>Diodora elevata</i> (Dunker, 1846) . .	R			+	+	+	+	+	+	+
† <i>Drillia tempestae</i> sp. nov.			+	+	+					
† <i>Epitonium lycocephalum</i> sp. nov. .				+					+	

Species	Habi- tat	W/E	50 m Complex					30 m Complex		
			TIL	BBR	USH	LSH	DLS (KN/SL)	USH	LSH	LSH (KL)
GASTROPODA (contd)										
† <i>Fasciolaria dinglei</i> sp. nov.					+					
† <i>Fissurella glarea</i> Carrington & Kensley, 1969	?R							+	+	
† <i>Fissurella robusta</i> Sowerby, 1892	R		+	+	+	+				
<i>Fissurellidea aperta</i> (Sowerby, 1825)	R						+			
<i>Fusus faurei</i> Barnard, 1959 (Koingnaas)			?	?	?	?	?			
<i>Gibbula zonata patula</i> ssp. nov. . .	R		+	+						
† <i>Haliotis saldanhae</i> Kensley, 1972	R				+		+			
<i>Helcion</i> sp.	R		+							
† <i>Hespererato oppenheimeri</i> Carrington & Kensley, 1969			?	?	?	?	?			+
<i>Littorina</i> sp.	R								+	+
<i>Marginella</i> sp.			+	+						+
<i>Melanella</i> sp.			+							
† <i>Melapium hawthornei</i> sp. nov. . . .							+			+
† <i>Namamurex odontostoma</i> Carrington & Kensley, 1969			+	+	+					
<i>Nassarius kochianus</i> (Dunker, 1846)		E								+
† <i>Nassarius litorafontis</i> Carrington & Kensley, 1969			?	?	?	?	?			+
<i>Natica</i> cf. <i>adansoni</i> Blainville, 1824	S/M	W								+
<i>Nucella dubia</i> (Kræuss, 1848)	R		+					+		
† <i>Nucella praecingulata</i> (Haughton, 1932)			+	+	+	+	+	+		+
† <i>Ocenebra bonaccorsii</i> Carrington & Kensley, 1969			+						+	
<i>Ocenebra purpuroides</i> (Reeve, 1845)	R		+							
† <i>Ocenebra petrocyon</i> sp. nov.									+	
<i>Oxystele sinensis</i> (Gmelin, 1791)	R	E	+	+	+	+	+	+		
<i>Patella argenvillei</i> Krauss, 1848	R		+	+	+			+		
<i>Patella barbara</i> Linnaeus, 1758 . . .	R		+	+	+			+		
<i>Patella granatina</i> Linnaeus, 1758 . .	R							+		
† <i>Patella hendeyi</i> sp. nov.	R			+	+					
† <i>Patella hoffmani</i> sp. nov.	R		+	+	+	+				
<i>Patella miniata</i> Born, 1778	R							+	+	
<i>Patella</i> sp.								+	+	
† <i>Pseudoliva lutulenta</i> sp. nov.							+			
<i>Ringicula turtoni</i> Bartsch, 1915 . . .		E					+			

Species	Habi- tat	W/E	50 m Complex					30 m Complex		
			TIL	BBR	USH	LSH	DLS (KN/SL)	USH	LSH	LSH (KL)
GASTROPODA (contd)										
<i>Sinum concavum</i> (Lamarck, 1822)		W							+	
† <i>Terebra canisaxi</i> sp. nov.				+	+		+			
† <i>Thais arenae</i> sp. nov.										+
<i>Tricolia capensis</i> (Dunker, 1846)	R		+	+						
† <i>Triumphis dilemma</i> Kilburn & Tankard, 1975			+	+	+					
† <i>Trophon carringtoni</i> sp. nov.					+					
<i>Tugali barnardi</i> (Tomlin, 1932) ...		E					+			
<i>Turbo cidaris</i> Gmelin, 1791	R		+	+	+	+	+	+	+	+
<i>Turritella carinifera</i> Lamarck, 1822	S			+	+			+	+	+
<i>Turritella declivis</i> Adams & Reeve, 1848		E					+			
† <i>Turris nigrovitta</i> Carrington & Kensley, 1969 (Koingnaas)			?	?	?	?	?			
<i>Vermetus</i> sp.			+	+			+	+	+	
BIVALVIA										
<i>Arca avellana</i> Lamarck, 1819	?R	E					+			
† <i>Arca halmyrus</i> Carrington & Kensley, 1969 (Strandfontein)	?R		?	?	?	?	?			
<i>Arca noae</i> Linnaeus, 1758	?R	W								+
<i>Aulacomya ater</i> (Molina, 1782) ...	R		+	+					+	
<i>Barnea truncata</i> (Say, 1822)	R	W					+		+	
† <i>Cardita unica</i> sp. nov.										+
† <i>Carditella calipsamma</i> Carrington & Kensley, 1969			+	+	+	+	+	+	+	
<i>Cardium</i> sp.							+			
† <i>Chamelea krigei</i> Haughton, 1926	S		+	+	+	+				
<i>Chlamys</i> sp.						+				
<i>Choromytilus meridionalis</i> (Krauss, 1848)	R							+		
† <i>Corbula palaegialis</i> (Carrington & Kensley, 1969) (Strandfontein)			?	?	?	?	?			
† <i>Cuna aquaedulcensis</i> Kensley, 1977									+	
† <i>Donax haughtoni</i> Carrington & Kensley, 1969	S		+	+	+	+				
† <i>Donax rogersi</i> Haughton, 1926 ...	S							+	+	
† <i>Dosinia sicarisinus</i> sp. nov.	S/M			+			+	+		
† <i>Gastrana fibrosa</i> Kilburn & Tankard, 1975	S				+					

Species	Habitat	W/E	50 m Complex					30 m Complex		
			TIL	BBR	USH	LSH	DLS (KN/SL)	USH	LSH	LSH (KL)
BIVALVIA (contd)										
† <i>Gastrana rostrata</i> Carrington & Kensley, 1969	S						+			
<i>Gastrana</i> sp.	S			+					+	
† <i>Glycymeris fulleri</i> sp. nov.	S						+			
? <i>Hiatella</i> sp.	R		+	+						
<i>Hinnites</i> sp.						+				
† <i>Isognomon gariesensis</i> sp. nov.						+	+			+
<i>Leporimetis hanleyi</i> (Dunker, 1853)	S/M	W					+		+	
<i>Lutraria</i> sp.	S/M			+	+	+	+		+	+
† <i>Macra</i> cf. <i>derenbergi</i> Böhm & Weisfermel, 1913	S/M									+
<i>Melliteryx capensis</i> (Sowerby, 1889)	RiS	E					+			
† <i>Notocallista schwarzi</i> (Newton, 1913)	S						+			
<i>Nuculana bicuspidata</i> (Gould, 1845)	S/M	W					+		+	
† <i>Ostrea</i> cf. <i>subradiosa</i> (Böhm & Weisfermel, 1913)	R				+					
<i>Perna perna</i> (Linnaeus, 1758)	R		+		+				+	
† <i>Petricola prava</i> Kilburn & Tankard, 1975	R			+					+	
<i>Phaxas decipiens</i> (Smith, 1904)	S/M		+	+					+	
<i>Scissodesma spengleri</i> (Linnaeus, 1767)	S			+						
† <i>Standella namaquensis</i> Carrington & Kensley, 1969	S		+	+	+				+	
<i>Striostrea margaritacea</i> (Lamarck, 1819)	R	E	+	+	+	+	+		+	+
<i>Tellina ponsonbyi</i> (Sowerby, 1889)	S/M	E			+				+	
<i>Tellina trilatera</i> Gmelin, 1791	S		+	+					+	+
<i>Theora</i> sp.	S						+			
<i>Tivela</i> cf. <i>compressa</i> (Sowerby, 1851)	S			+	+				+	
<i>Venus verrucosa</i> Linnaeus, 1758	S	W		+	+				+	+
SCAPHOPODA										
<i>Dentalium</i> sp.	S/M						+			
POLYPLACOPHORA										
<i>Chaetopleura pertusa</i> (Reeve, 1847)	R		+							
cf. <i>Chiton</i> sp.	R		+	+	+		+		+	
cf. <i>Dinoplax</i> sp.	R		+							

Table 1 indicates the preferred habitats of most species. In a number of cases there is uncertainty about habitat, especially for extinct species. While most are open-coast forms, there are calm-water components present (e.g. *Bullia laevissima*, *Phaxas decipiens*, *Dosinia sicarisinus*, *Lutraria* sp., *Leporimetis hanleyi*). Among the open-coast forms, rocky-shore species outnumber sand and mud inhabitants almost two to one. Among the rocky-shore forms are a number of grazers and algal inhabitants such as *Haliotis*, *Crepidula*, *Oxystele*, *Turbo*, *Calliostoma*, and *Patella*. Predators such as *Argobuccinum*, *Namamurex*, *Thais*, *Ocenebra*, *Conus*, and *Terebra* are also abundant. Filter feeders such as *Turritella*, scavengers like *Bullia* and *Nassarius*, and parasitic forms such as *Epitonium* and *Melanella* are also present, indicating a rich and diverse environment with numerous habitats. Of the sand and mud dwellers there are suspension and filter feeders (*Donax*, *Dosinia*, *Scissodesma*, *Venus*, *Lutraria*), as well as deposit feeders (*Tellina*).

Of the species recorded by Carrington & Kensley (1969), only four have not been found during the present study. These are *Fusus faurei*, *Turris nigrovitta*, *Corbula palaegialis*, and *Arca halmyrus*, all recorded from the 50 m Complex. *Nassarius litorafontis* and *Hespererato oppenheimeri*, recorded from the 50 m Complex by Carrington & Kensley (1969), have been found in the 30 m Complex in this study.

ZOOGEOGRAPHIC AFFINITIES

There is a small west African–Mediterranean component of nine species in the faunal list: *Arca noae*, *Barnea truncata*, *Cantharidus (Jujubinus) striatus*, *Crepidula porcellana*, *Leporimetis hanleyi*, *Nuculana bicuspidata*, *Natica* cf. *adansoni*, *Sinum concavum*, *Venus verrucosa*. Of these, *Arca noae*, *Cantharidus (Jujubinus) striatus* and *Natica* cf. *adansoni* are strictly West Africa–Mediterranean in distribution; the present fossil records are the most southerly for all three. *Nuculana bicuspidata* occurs live in West Africa, and is known as a Pleistocene fossil from Velddrif (Kruispad), Table Bay (Milnerton), and Port Elizabeth (Redhouse) (See Kilburn & Tankard 1975: 206). *Leporimetis hanleyi* is known live from Luanda, while an isolated population occurs at Sandvis, just south of Walvis Bay. It is recorded as fossil in the Late Pleistocene in the Saldanha area, and also at Redhouse, Knysna, Sedgfield, and Klein Brak River. *Venus verrucosa* and *Crepidula procollana* both occur from North Africa, around the Cape, to Natal. *Barnea truncata* is known from the Late Pleistocene of Table Bay (Kensley 1985a) and also from fresh dead shells washed ashore at the same locality. *Sinum concavum* is an extant West African species, known from Senegal to Angola (Nicklés 1950). This so-called West African component thus represents a mix of widespread temperature-tolerant species, as well as less temperature-tolerant forms now restricted to more tropical areas.

The present-day distribution of living species represented in the faunal list shows a majority of forms (27 species, 29 %) occurring on both east and west coasts of southern Africa. Only 11 species are at present restricted to the east

coast: *Calyptraea helicoidea*, *Melliteryx capensis*, *Nassarius kochianus*, *Oxystele sinensis*, *Ringicula turtoni*, *Arca avellana*, *Striostrea margaritacea*, *Tellina ponsonbyi*, *Tugali barnardi*, *Turritella declivis*, *Cylichna tubulosa*. Of these, only the Indo-Pacific *Arca avellana* has a distribution extending north of southern Mozambique.

The inferring of past sea-temperature regimes based on the known temperature ranges of living species is a complex issue fraught with pitfalls. Some guidelines do exist. Tankard (1975b: 33) presented temperature minima for a range of Pleistocene molluscs of South Africa, and indicated a warm-water affinity for a number of west-coast fossils. Several of these occur in the present suite:

	Temperature minima
<i>Nuculana bicuspidata</i>	17°C
<i>Scissodesma spengleri</i>	14°C
<i>Tellina ponsonbyi</i>	14°C
<i>Leporimetis hanleyi</i>	17°C

Kilburn & Rippey (1982) mention that *Striostrea margaritacea* spawns when monthly average temperatures exceed 20°C.

Examining the nine 'West African', and the 11 east-coast forms (with their implied warmer-water requirements), it is seen that 7 species, including *Striostrea margaritacea* and *Nuculana bicuspidata*, occur in both the 50 m and 30 m Complexes. Fourteen of the 20 species occur in the 50 m Complex, 12 in the 30 m Complex. It is thus inadvisable to attribute a colder temperature regime to the 30 m Complex and a warmer regime to the 50 m Complex. Nevertheless, there is undeniably a component showing a warm-water bias in the present suite of fossils, deduced from known temperature ranges of living species. The temperature requirements for the extinct forms, with the greater preponderance of species in the 50 m Complex, can only be guessed at. The reasons for the extinction of these forms are probably related in part to sea-temperature changes.

An ocuulinid coral, found encrusting rocks at Hondeklip in 50 m Complex exposures, and tentatively identified as *Schizoculina fissipara* (Milne Edwards & Haime), casts further light on the question of temperature regimes. According to Laborel (1974), modern *S. fissipara* is adapted to low-salinity, warm, Guinean waters, and has a ramose morphology. However, encrusting to subramose forms (as in the present case) occur at the extremes of its range where periodic upwelling takes place. This instance probably represents the most southerly occurrence of *S. fissipara* in the fossil record and implies the extension of tropical water southward to Hondeklip latitudes. Lithological evidence of upwelling off Hondeklip during 50 m Complex times comes from phosphorite rinds interbedded with regressive storm gravels deposited in the bedrock-defined embayment during the earlier stages of bedrock emergence, prior to the establishment of back-barrier conditions. The thin phosphorite rinds mark intervening

fairweather periods during the deposition of the storm gravel. Hondeklip was probably situated adjacent to a marine regime characterized by the interaction of upwelling and south-flowing tropical currents during the period of deposition of the 50 m Complex.

The warm-water species common to both the 50 m and the 30 m Complexes, especially the abundant *Striostrea margaritacea*, undoubtedly point to a sea-temperature regime considerably higher than that prevailing on the west coast at present. Over the period of deposition of both complexes, however, a cooling trend must be inferred from the presence of numerous species living at present on the west coast. The apparent reduction in diversity reflected by the 30 m Complex may be indicative of cooling. Significantly, *Choromytilus meridionalis* evidently first appears during 30 m Complex times (Early Pleistocene). The cooling trend is also indicated by the extinction of *Striostrea margaritacea* on the west coast subsequent to the Early Pleistocene.

The Hondeklip fossil fauna probably represents a mixture of forms at different points in their history, reflecting both the influence of the cold Benguela system and subtropical waters, fluctuating, glacially controlled sea-levels and temperatures, along with varying temperature requirements. Thus, some specimens may represent the last members of a population that was dying out owing to decreasing temperatures, others a population adapting to fluctuating conditions, others an 'experimental' pioneering stock having tenuous reproductive success, and still other temperature-tolerant and actively reproducing populations.

FAUNAL COMPARISONS

Evaluation of the fauna from Hondeklip and vicinity must necessarily take the following into consideration.

The faunal list is undoubtedly incomplete. An unavoidable bias is, of course, the very nature of the geological record. Only deposits accumulated during regression from the sea-level maxima are available for examination; deposits closer to the regressive maxima are not available, nor are deposits of the transgressions. Thus the sedimentary packages available for sampling were deposited during the earlier stages of recovery from major polar deglaciations. In this sense successive complexes are somewhat directly comparable, but this may also make for the reduction of faunal dissimilarity between complexes. Original community patchiness, differential transport, preservational bias due to dissolution, and sampling bias (e.g. the tendency for small forms to be overlooked) all contribute to an incomplete faunal list.

The latitudinal ranges of species in deposits equivalent to the 50 m and 30 m Complexes are largely unknown or uncertain. Sampling was restricted to a few localities in close proximity.

The temporal ranges of species are similarly unknown or uncertain. The Late Tertiary and Middle Pleistocene are practically unsampled. The best comparative faunal lists exist for the Late Pleistocene (e.g. Tankard 1975a; Kensley 1985a).

In spite of these limitations, comparisons with other west-coast assemblages are instructive.

Bogenfels Tertiary Deposits

While the overall fauna of the Tertiary deposits of Bogenfels, South West Africa–Namibia, is distinctive and very different from any present-day assemblage (Böhm & Weisfermel 1913; Böhm 1926) there are a few elements that hint at a distant relationship with the Hondeklip suite.

The presence of a species of *Pseudoliva* (with one living species in West Africa, and two extinct species from Bogenfels), mactrid hinges closely resembling *Mactra* (*Barymactra*) *dermburgi* Böhm & Weisfermel from Bogenfels (Fig. 42), and a single oyster valve almost identical with *Ostrea subradiosa* Böhm (Fig. 35) suggest that there may well be Tertiary stragglers or their descendants in the Hondeklip assemblage. This suggestion, however, must be treated as highly speculative.

Marine Neogene of Ysterplaat

Tankard (1975a) provided a list of 13 molluscs recovered from the Miocene of Ysterplaat, Cape. Olson (1985), on the basis of fossil penguin material from the same locality, placed the assemblage in the Early Pliocene. The bivalves *Cardium edgari* Newton, 1913, and *Glycymeris borgesii* (Cox, 1939) support a Neogene age. Also taken from the Ysterplaat site were *Donax serra* Dillwyn, 1817, *Scissodesma spengleri*, *Dosinia lupinus* and a *Pitar*, since identified as *Notocollista schwarzi*. Of these all but *Donax serra* and *Dosinia lupinus* occur at Hondeklip. While most of the Ysterplaat *Dosinia* specimens are within the usual size range of *D. lupinus*, a few reach the size of *D. sicarisinus* described above. Unfortunately, the Ysterplaat material is all mouldic, and a clear impression of hinge and mantle details is lacking, making a positive identification difficult. *Donax serra* is discussed in the next section.

Early Pliocene molluscs from Langebaanweg, Cape

Kensley (1972, 1977) recorded a number of molluscs from Langebaanweg, several of which also occur at Hondeklip. These are *Cuna aquaedulcensis*, *Bullia digitalis*, *B. laevisima*, *Tricolia capensis*, *Haliotis saldanhae*, and *Thais dubia*. *Cuna aquaedulcensis* is locally abundant in the 30 m Complex at Hondeklip. *Bullia digitalis* is abundant in both the 30 m and 50 m Complexes; its living range from South West Africa–Namibia to Transkei would indicate that this is a temperature-tolerant species, and its presence in deposits from the Pliocene to the Holocene is not surprising.

The fossil distribution of *Donax serra*, however, is difficult to explain. It has been recorded from the Pliocene of Ysterplaat (Tankard 1975a), and Langebaanweg (Kensley 1972, 1977), and the Pleistocene of Lüderitz, Orange River mouth, Velddrif, Sedgfield (Barnard 1962), and Table Bay (Kensley 1985a). It has not been seen in the Hondeklip deposits under discussion, where *D. rogersi* (30 m

Complex) and *D. haughtoni* (50 m Complex) are both abundant. Its present-day distribution is from South West Africa–Namibia to Transkei, while De Villiers (1975) reported the species to reproduce in a temperature range of 13–17°C. Inappropriate temperature thus seems unlikely to be the reason for its absence from the Hondeklip area. It is possible that local competition from the two extinct species during the Early Pleistocene precluded the establishment of a population of *D. serra* in the Hondeklip area.

Verlorevlei–Saldanha Pleistocene deposits

A number of species recorded from the Pleistocene of the south-western Cape around Verlorevlei and Saldanha (Kilburn & Tankard 1975) are present in the Hondeklip assemblage. The extinct species *Petricola prava*, *Nucella prae-cingulata*, *Triumphis dilemma* and *Fissurella robusta* were obtained from deposits at 10 masl at Saldanha Bay. The latter two species occur in the 50 m Complex and the former two in both the 50 m and the 30 m Complexes at Hondeklip. *Cerithidea bifurcata* Kilburn & Tankard, 1975, an extinct species also obtained from the 10 masl deposit, has not yet been found in Namaqualand.

Tankard (1975c) correlated the Saldanha deposit at 10 masl with the 50 m Complex in Namaqualand on the basis of the four species mentioned above. The presence of *Fissurella robusta* and *Triumphis dilemma* suggests that this correlation may be correct but it should be verified by additional criteria. Accepting the equivalence of the deposits, comparison of the faunal lists shows an additional 13 extant species in common with the 50 m Complex at Hondeklip, all of which occur on both west and east coasts. Of the Saldanha fauna, only *Patella tabularis* Krauss, 1848, *P. concolor* Krauss, 1848, and *Peristernia nassatula* (Lamarck) are south- and east-coast species not present off Saldanha today. Tankard (1975c) attributed the absence of *Striostrea margaritacea* and *Donax haughtoni* from the Saldanha deposit to colder water conditions there during the 50 m Complex times.

Gastrana fibrosa, a probably extinct species recorded from the Late Pleistocene in the south-western Cape, extends back into the Late Pliocene in central Namaqualand, as shown by its occurrence in the 50 m Complex. The extinct Late Pleistocene species *Crepidula capensis praerugulosa* Kilburn & Tankard, 1975, is not present in the Hondeklip assemblage, though *Crepidula porcellana* is.

CONCLUDING REMARKS

Significantly, the warm–cold distinction between the 50 m and 30 m Complexes respectively (or across the Plio–Pleistocene boundary), is not clear-cut on the basis of existing data, due to the considerable faunal similarity between the complexes. Notably, there are 34 species (11 extinct) common to both complexes. Of the species unique to the 30 m Complex, only five are relatively abundant, viz. *Donax rogersi*, *Fissurella glareata*, *Choromytilus meridionalis*, *Cuna*

aquaedulcensis, *Ocenebra petrocyon*. The reduction of diversity and the appearance of *Choromytilus meridionalis* may suggest a cooler regime during 30 m Complex times, relative to the 50 m Complex.

The value of *Donax haughtoni* and *Donax rogersi* as zone fossils for the 50 m and 30 m Complexes, respectively, is verified in this study. *Donax haughtoni* is present at least as far south as the Olifants River. *Donax rogersi*, the 30 m Complex zone fossil, is present at least as far south as Doringbaai and has been found as far north as Walvis Bay (pers. obs.). However, there are no faunal lists from 30 m Complex correlates in the south-western Cape for comparison. It appears that only subsequent to the Early Pleistocene did the Namaqualand west-coast mollusc fauna more closely resemble the modern fauna. This probably reflects the increasing dominance of the Benguela system and restriction of warmer waters to the north, the cooler regime facilitating a species radiation northwards from the south-western Cape. The ecological niche of *Striostrea margaritacea* was usurped, to some extent, by the mytilids and patellids, the latter to become an important food resource of early man on the west coast. The first appearance of *Patella compressa*, the kelp limpet, already present by the Late Pleistocene, is an important datum yet to be established.

Sedimentological aspects of the complexes suggest that, in the Hondeklip area during 50 m Complex times, the coast was characterized by a sea-level interaction with the bedrock topography that resulted in an embayed coast concomitant with conditions for the development of extensive back-barrier environments. In contrast, the 30 m Complex is characterized by relative insulation from antecedent topographic effects, resulting in a more exposed coastal regime. Superimposed upon these littoral influences are the effects of the adjacent oceanographic temperature regime. Thus a secure database from which to deduce Late Cenozoic palaeoclimatic influences will only exist once the regressive packages are examined sedimentologically and faunistically sampled on a regional basis in order to resolve the large-scale changes in the boundaries of marine zoogeographic provinces in time, to recognize the environmental vectors such as depositional palaeodepth and possibly thermally anomalous lagoons, and allied to the latter, to evaluate the roles of antecedent topography and sediment supply.

In conclusion, this study suggests that molluscs have potential for a significant contribution in the unravelling of Late Cenozoic history. More extinct molluscs were found than expected and the relatively high level of endemism holds promise that more zone fossils may emerge. The extant component of the fauna permits some extrapolations of temperature tolerances and environmental preferences. An overall cooling trend is reflected in the approach of successively younger assemblages towards the modern west-coast faunal composition.

Comparison of Palaeogene, Neogene, Quaternary, and extant faunas suggests that extinction, speciation, and migratory colonizations were staggered as a reflection of differing temperature tolerances, habitat creation-destruction, and competition. However, a regional mollusc-assemblage zonation scheme must

in time necessarily be supplemented by zonations of ostracode and benthic foraminiferal assemblages. Planktonic Foraminifera are evidently very scarce in these littoral deposits, while nannoplankton has not yet been collected, but efforts to recover these microfossils may aid correlation with deep-sea data and the global record. Resolution of the tectonic component of the coastal-plain marine record awaits reliable regional correlations.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers.

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- (a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...': '... in *C. namacolus* (Fig. 10) ...'
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e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
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e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should preferably be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

BRIAN KENSLEY

&

JOHN PETHER

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FOSSIL MOLLUSCA OF THE HONDEKLIP AREA,
CAPE PROVINCE, SOUTH AFRICA

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Title: informative but concise, without abbreviations and not including the names of new genera or species
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- (c) *Table of contents* giving hierarchy of headings and subheadings
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3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 3 cm margins all round. First lines of paragraphs should be indented. Tables and a list of captions for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

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Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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The number of the figure should be lightly marked in pencil on the back of each illustration.

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FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74** (33): 627–634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2** (17): 309–320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* **17** (4): 1–51.

THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

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THE SOUTHERN BENGUELA REGION
PART 1
FAUNAL COMPLEXITY AND DISTRIBUTION

By
P. ALEXANDER HULLEY

Cape Town Kaapstad

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PART 1

FAUNAL COMPLEXITY AND DISTRIBUTION

By

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(With 2 figures and 8 tables)

[MS accepted 27 February 1986]

ABSTRACT

Various sampling cruises in the southern Benguela region (28°40'S–40°00'S 10°00'E–20°00'E) yielded a total of more than 17 000 lanternfishes (family Myctophidae). These comprise 65 species in 23 genera. Their horizontal distribution in the region is discussed in terms of their known Atlantic and Indo-Pacific ranges and their vertical distribution in relation to oceanic and pseudo-oceanic zonation. Results indicate that inshore of the 300 m isobath, lanternfishes are represented by a single, pseudo-oceanic species, *Lampanyctodes hectoris*. Oceanic species occur where bottom depths exceed this value. The sampling strategies employed preclude investigation of the diurnal relationship between mesopelagic and bathypelagic species. The southern Benguela region can be characterized as a transition zone rather than a subtropical zone. There is a strong intrusion of convergence and semisubantarctic species in association with cold-core eddies from the south, and a much weaker advection of tropical and broadly tropical species in Agulhas Water. A first estimate of the offshore lanternfish stock for the eastern South Atlantic is calculated as $8\text{--}12 \times 10^6$ tonnes which represents 50–70 per cent of the total estimated mesopelagic fish stock of the offshore eastern South Atlantic.

CONTENTS

	PAGE
Introduction.....	227
Material and methods.....	229
Results.....	230
Discussion.....	238
Acknowledgements.....	246
References.....	246

INTRODUCTION

In order to assess the status of commercially exploited marine resources, the Sea Fisheries Research Institute (SFRI), Cape Town, has an ongoing series of routine sampling cruises in the eastern South Atlantic. Material and data arising from these cruises play a significant role in the CSIR–SANCOR-sponsored Benguela Ecology Programme, in which the structure and dynamics of the

Benguela Upwelling System is being investigated. Lanternfishes (family Myctophidae) are a regular and abundant component of the catch from both the pelagic and benthic sampling. They represent not only an important group of trophic organisms within the system, but also represent an alternative fishery resource to more conventional species like anchovy (*Engraulis capensis*) and pilchard (*Sardinops ocellata*).

Ahlstrom *et al.* (1976) reported that in the eastern Atlantic myctophids comprise nearly 10 per cent of all fish larvae caught between 19° and 26°S, with larval abundance values greater than 10 larvae/m² for the period August 1973 to April 1974. Recent surveys have indicated a larger proportion of myctophid larvae (29%) in Bongo net catches off the west coast (R. A. Cruickshank pers. comm.). Lanternfishes (mainly *Lampanyctodes hectoris*) were first recorded in the South African purse-seine catches in 1969, when 1 134 tons were taken (0,3% of the total catch). Subsequently, the catch has fluctuated, with a maximum of 42 560 tons being taken in 1973 (10,45%) (De Villiers 1982). A fishing quota of 50 000 tonnes has been allocated for the 1985 season.

Hulley (in press) has pointed out that there are 28 genera and 125 species of myctophid known, or likely to be found, in the southern African region, and has given a general account of their taxonomy and distribution. Some results have also been presented on the myctophid fauna of the southern Benguela region (Hulley 1972a, 1972b, 1981, 1986), but data from recent cruises allow for a more critical investigation of the structure and distribution of the lanternfish fauna. Rubiés (1985) has recently examined the myctophid fauna off the South West African–Namibian coast, recording a total of 41 species. Twenty-five of these species were taken only from the Valdivia Bank area on the Walvis Ridge, ten species only from the Benguela area, and six species were common to both areas.

The purpose of this paper is threefold: firstly, to establish the myctophid species complexity in the southern Benguela region, i.e. between 28°40'S (mouth of the Orange River) and 40°00'S, and between 10°00'E and 20°00'E; secondly, to examine the nature of the distribution patterns of these species, including both the oceanic and pseudo-oceanic zones; and thirdly, to obtain a first estimate of lanternfish abundance in the offshore area (greater than 100 miles offshore) of the South-east Atlantic. Here the total offshore mesopelagic fish stock has been estimated at 16×10^6 tonnes (Gjøsaeter & Kawaguchi 1980).

Investigations of the biology of *Lampanyctodes hectoris*, leading to estimates of inshore lanternfish abundance for the same region, are to be made independently by scientists at the Sea Fisheries Research Institute, Cape Town; these will be reported separately.

The areal choice in the present paper should also allow for the examination of distributional phenomena across the frontal zone(s) between upwelled Benguela Water and South Atlantic Central Water in the region of the shelf break at 300–500 m (Shannon 1985), but this aspect will be more fully developed in later publications.

MATERIAL AND METHODS

Specimens and data on specimens from the following cruises and from stations occupied with the following gear within the region have been incorporated into the analysis:

Walther Herwig 1971—Transect II	(WH-71)	MT-1600	(March)
Walther Herwig 1971—Transect II		David Net	(March)
SFRI Hake Survey 1984	(HJUL84)	BT-180	(July)
SFRI Hake Survey 1985	(HJAN85)	BT-180	(January)
SFRI Phyllosoma Survey 1982	(PAUG82)	RMT-2	(August)
SFRI Phyllosoma Survey 1983	(PAUG83)	RMT-8	(August)
SFRI Phyllosoma Survey 1984	(PAUG84)	RMT-8	(August)
SFRI Anchovy Acoustic Survey 1983	(ANAC83)	RMT-8	(May)

In addition, the lanternfish material in the collections of the South African Museum, Cape Town, taken within the defined southern Benguela region, has been re-examined for the purposes of this paper. These specimens were taken with a variety of gear-types: neuston net; N100B; N200B; IKMT.

Gear-type abbreviations are as follows:

BT-180: German bottom trawl with 180' headline and stocking

David net: modified David neuston sampler

IKMT: 10' Isaacs-Kidd midwater trawl

MT-1600: Engel midwater trawl with 1 600-mesh circumference

RMT-2: rectangular midwater trawl with 2 m² mouth opening

RMT-8: rectangular midwater trawl with 8 m² mouth opening

All specimens were identified to species. Standard lengths (SL), and in certain instances preserved wet weights, were taken for each specimen, resulting in data on more than 17 000 specimens. Taxonomic details for individual species are not given. However, the *Smith's sea fishes* (SFSA) species number (Hulley in press) is given, so that readers may refer to that publication for those details.

For all cruises, daytime hauls were distinguished from night hauls on the basis of commencing after 06h00 or before 18h00 (local time). Myctophids were absent from six (86%) of the day hauls from PAUG82 and eight (57%) day hauls from PAUG83; no day hauls were undertaken during PAUG84. For the purposes of stock estimation, distribution pattern and subpattern catch rates (specimens/hour) were calculated for night hauls only, according to the method of Hulley & Krefft (1985), for species from each of the RMT-2 (PAUG82) and RMT-8 (PAUG83 and PAUG84) nets, and for both day (1 haul, fishing depth >1 000 m) and night hauls for species from the MT-1600 (WH-71) net. These catch rates were converted into abundances in specimens/1 000 m³, assuming that each gear was 100 per cent effective for the duration of the haul, that the fishes were evenly distributed in the upper 1 000 m, and that the mouth areas and mean trawling speeds were 2 m² and 2.5 knots (RMT-2), 8 m² and 2.5 knots (RMT-8), and 300 m² and 3.5 knots (MT-1600). On the basis of SL/weight scatter plots for *Lampanyctodes hectoris* (Fig. 1) and inspection of the

standard lengths of specimens taken by each gear, the mean weight of a fish from the RMT-2 samples was accorded a value of 0,2 g, from the RMT-8 samples a value of 0,5 g, and from the MT-1600 samples a value of 1,0 g. The area of the offshore South-east Atlantic region is taken as $160 \times 10^{11} \text{ m}^2$ (Gjøsaeter & Kawaguchi 1980).

RESULTS

Haul data, which includes discrimination by depth and/or time of day, is given in Tables 1 to 6. Positive hauls indicate the presence of myctophids. Table 7 is a species list of Myctophidae for the southern Benguela region and incorporates the Atlantic distribution pattern and subpattern placement of each species according to Hulley (1981), the number of specimens examined for each species, and the SFSA species number.

BT-180

Catch data for this gear (Tables 1, 2) indicate that although sampling was carried out from depths less than 101 m to greater than 500 m, the major fishing effort was concentrated between depths of 101–200 m (35% of total) and 210–300 m (30–35%). During both cruises, stations were occupied mainly during daylight hours (95% of total number). Therefore, although the results for night hauls should be regarded as tentative, it would appear that the epibenthic (pseudoceanic) lanternfish fauna exhibits diurnal migration into the water column during this period, since no specimens were taken during the night at depths of maximum daytime abundance (101–300 m). Furthermore during the day myctophids were taken only in 41–52 per cent of the hauls, pointing to the possibility of an extremely patchy distribution (see below). The major component of the lanternfish catch throughout the year was *Lampanyctodes hectoris*, whose highest mean catch rates were in the 101–200 m and 210–300 m depth ranges. Day mean catch rates at these depths were 4,9 and 5,6 specimens/hour respectively in winter, and >153,9 and 73,6 specimens/hour respectively in summer, suggesting a marked seasonal variation in availability and/or distribution. More recent unpublished data from the winter (July) 1985 Hake Survey support this suggestion. In the 301–400 m, 401–500 m and >500 m depth strata, mean catch rates for *Lampanyctodes hectoris* were considerably lower (winter: 7,7; 1,1; 0,3 specimens/hour; summer: >13,8; >2,9; 0,0 specimens/hour respectively). Other myctophid species were taken in those bottom hauls fished at depths greater than 301 m (*Diaphus hudsoni* (2 specimens), *D. meadi* (1), *D. ostenfeldi* (1), *Electrona risso* (2), *Gymnoscopelus (Nasolychnus) piabilis* (2), *Scopelopsis multipunctatus* (1), *Symbolophorus barnardi* (4), *S. boops* (7)) but these probably represent contaminants as the net is heaved from depth, since mean catch rates for the individual species range only between 0,1 and 1,0 specimens/hour ($\bar{x} = 0,3$ specimens/hour) and there is a decrease in the percentage of negative hauls at depths below 301 m. The high percentage of

TABLE 1

Analysis of myctophid data from BT-180 net during SFRI Hake Surveys.
= number of hauls; + = number of positive hauls; - = number of negative hauls.

Cruise	Time (local)	Total		0-100 m		101-200 m		201-300 m		301-400 m		401-500 m		> 500 m	
		#	+	#	+	#	+	#	+	#	+	#	+	#	+
HJUL84	0600-1800	86	25	61	4	0	4	31	9	22	29	5	24	10	4
	1800-0600	2	0	2	0	0	0	0	0	0	2	0	0	0	0
HJAN85	0600-1800	100	34	66	10	0	10	34	9	25	29	10	19	13	5
	1800-0600	7	0	7	0	0	0	3	0	3	3	0	3	0	0

TABLE 2

Analysis of myctophid data from BT-180 net during SFRI Hake Surveys.
= number of hauls; SP = number of species; SPP = number of specimens.

Cruise	Total		Time (local)	0-100 m		101-200 m		201-300 m		301-400 m		401-500 m		> 500 m	
	#	SPP		#	SPP	#	SPP	#	SPP	#	SPP	#	SPP	#	SPP
HJUL84	88	6	0600-1800	4	0	0	31	1	152	29	1	163	10	2	79
		417	1800-0600	0	0	0	0	0	0	2	0	0	0	0	0
HJAN85	107	6	0600-1800	10	0	0	34	1	>5234	29	1	>2135	13	4	>182
		7585	1800-0600	0	0	0	3	0	0	3	0	0	0	0	0

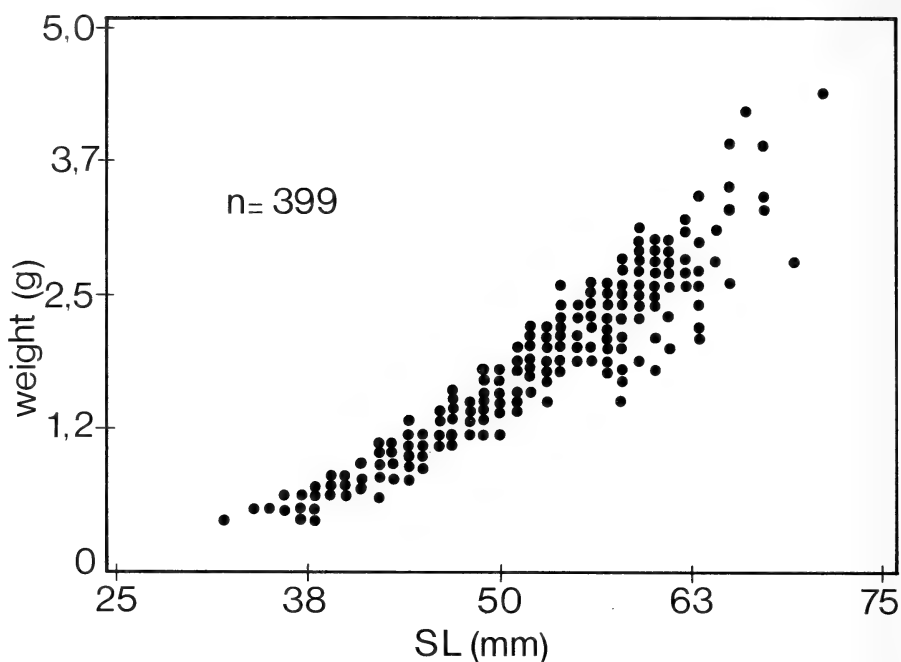


Fig. 1. Scatter plot of standard length (SL) versus preserved wet weight for *Lampanyctodes hectoris*.

negative hauls in the 101–200 m (71–73%) and 201–300 m (66–83%) depth strata can therefore only be accounted for by the absence of a single species, *Lampanyctodes hectoris*, and Index of Dispersion (ID) values (Wormuth & Roper 1983) considerably greater than 1.0 indicate that the distribution of *Lampanyctodes hectoris* is strongly patchy within its principal epibenthic distributional depth range (101–300 m). Further development of the data for this species is outside the scope of the paper, although it should be mentioned that *Lampanyctodes hectoris* was also taken in pelagic hauls, particularly those inside or immediately adjacent to the frontal system developed by the upwelled Benguela Water. These specimens are probably associated with the system of cold-core eddies generated at the front (Lutjeharms 1981a).

RMT-2 and RMT-8

Catch data for these nets from the SFRI Phyllosoma Surveys (PAUG82, PAUG83 and PAUG84) are given in Tables 3 and 4. The major sampling effort was directed at depths between 200–0 m and 75–0 m (63% of total) and only one haul was made below 500 m (day). RMT-2 nets also sampled the 10–0 m (11%) and 50–0 m (16%) strata—depths not specifically fished during the 1983 and 1984 RMT-8 sampling programme, although nine oblique hauls were made with the latter gear from a maximum depth of 250 m.

TABLE 3

Analysis of myctophid data from RMT-2 and RMT-8 nets during SFRI Phyllosoma Surveys. A = number of hauls with opening-closing device fitted; B = number of oblique hauls to fishing depth; SP = number of species; SPP = number of specimens.

[illegible]

TABLE 4
Analysis of myctophid data from RMT-2 and RMT-8 nets during SFRI Phyllosoma Surveys.
= number of hauls; + = number of positive hauls; - = number of negative hauls.

Gear Year	#	Time (local)	Total		Group A		Group B		Group C		Group D		Group E							
			#	+	-	#	+	-	#	+	-	#	+	-						
RMT-2 1982	71	0600-1800	7	1	6	1	0	1	0	0	0	5	1	4	1	0	1	0	0	0
		1800-0600	64	57	7	13	8	5	19	18	1	32	31	1	0	0	0	0	0	0
RMT-8 1983	27	0600-1800	14	6	8	0	0	0	0	0	0	4	2	2	9	4	5	1	0	0
		1800-0600	13	12	1	0	0	0	0	0	0	12	11	1	1	1	0	0	0	0
RMT-8 1984	24	0600-1800	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		1800-0600	24	23	1	0	0	0	0	0	0	24	23	1	0	0	0	0	0	0

RMT-2 data reveal a high proportion of negative daytime hauls (86% of PAUG82 cruise), the single positive sample (09h50: 150–0 m) yielding four specimens each of *Diaphus hudsoni* and *Lampanyctus lepidolichnus*. Negative daylight hauls with the RMT-8 were lower (57%) during the 1983 cruise (PAUG83); no daytime sampling was undertaken during PAUG84. Two positive daytime hauls (P 011: 06h31–07h31; P 024: 15h00–16h00) were made in the 200–0 m depth range during PAUG83 and yielded a total of 38 specimens (*Benthoosema suborbitale*, *Ceratoscopelus warmingii*, *Diaphus hudsoni*, *D. meadi*, *Lampanyctus pusillus*, *Lobianchia dofleini*, *Metelectrona ventralis*, *Symbolophorus boops*), while 102 specimens were recorded from the four positive daytime stations in the 500–0 m depth range during the same cruise. The species recorded at these latter stations were *Benthoosema suborbitale*, *Ceratoscopelus warmingii*, *Diaphus effulgens*, *D. hudsoni*, *D. lucidus*, *D. meadi*, *D. metopoclampus*, *D. ostenfeldi*, *Diogenichthys atlanticus*, *Hygophum hygomii*, *Lampadena notialis*, *Lampanyctus alatus*, *L. pusillus*, *Lobianchia dofleini*, *Protomyctophum (Hierops) subparallelum*, *Scopelopsis multipunctatus* and *Symbolophorus barnardi*.

For night sampling, 89 per cent and 92–96 per cent of stations occupied with the RMT-2 and RMT-8 respectively, yielded lanternfishes. No definite scattering layer was observed at station 9 (4)—the single negative night station of the PAUG84 cruise, while the single negative night haul (P 003: 04h13–05h13) from the PAUG83 cruise was in 120–0 m. Seven negative night hauls were recorded during PAUG82, five (71%) of which were 10–0 m or at the surface; the net bar was bent during the single negative night haul (Station Number 002030) in the 50–0 m depth range. The number of hauls, number of species, and number of specimens for both gear during the PAUG82, PAUG83, and PAUG84 cruises is summarized in Table 3.

RMT-8 data from ANAC83 are included in Table 6. A total of 2 248 specimens was taken during this cruise, in which the net was aimed at target species, the duration of the haul being one hour, and the maximum fishing depth not exceeding 100 m. Thirty-eight specimens of *Lampanyctodes hectoris* from four hauls lack accurate depth data but have been included at the 0 m depth only for the sake of completeness. The four hauls in the 50–0 m fishing-depth range yielded 643 specimens of one species (*Lampanyctodes hectoris*), but 35 hauls in the 100–0 m range caught 1 563 specimens of *Lampanyctodes hectoris*, two *Diaphus hudsoni*, and one specimen of each of *Diaphus meadi* and *Hygophum hanseni*. Further analysis of these data has revealed that species other than *Lampanyctodes hectoris* were caught in the upper 100 m only at those stations where the bottom soundings were in excess of about 500 m.

For *Lampanyctodes hectoris*, the highest mean catch rate (130,14 specimens/station; number of stations = 7) was obtained inside of the 100 m isobath. Between the 100 m and 200 m isobaths the mean catch rate was 52,76 specimens/station ($n = 21$); between 200 m and 300 m, 34,00 specimens/station ($n = 3$); between 300 m and 400 m, 15,25 specimens/station ($n = 4$);

between 400 m and 500 m, 11,33 specimens/station ($n = 3$); and greater than 500 m, 3,33 specimens/station ($n = 3$). These data suggest that, for RMT-8 hauls at least, the major pelagic concentrations of *Lampanyctodes hectoris* are shoreward of the 100 m isobath and that ID values are considerably greater than 1, i.e. a marked patchiness.

During this same cruise, two hauls were made at the surface with a neuston net and yielded a total of 147 *Symbolophorus boops*, five *Symbolophorus barnardi*, and one *Lampanyctodes hectoris*. Both hauls were deployed over bottom depths of 510–640 m.

MT-1600

During the course of Transect II of the 1971 cruise of FRV *Walther Herwig*, six stations were occupied in the defined area with an MT-1600 net (Table 5). Shallower hauls (112–0 m, 305–0 m, 592–0 m) were made at night, while a single deep haul (>1 000–0 m) was made during the day. A total of 2 310 specimens in 46 species was taken. Of these species, only *Diaphus richardsoni*, *Electrona carlsbergi*, *Lampanyctus lineatus* and *L. nobilis* were not collected by the other types of gear. *Lampanyctodes hectoris* was not recorded from any of the MT-1600 stations, which were situated at distances of greater than 95 sea miles offshore, where bottom depths exceeded 3 500 m. Hulley (1981) gave a breakdown of the species distributions at these stations.

Other gear

The myctophid specimens taken in the southern Benguela region during the deep-sea cruises of *Africana II* (Table 6: N200B, IKMT_a) have been described by Hulley (1972a). The nine IKMT oblique hauls (5 day; 2 night; 1 day–night (15h25–19h10); and 1 time unknown) from 1 000–0 m yielded 138 specimens comprising 29 species, while the single IKMT oblique haul (day) from 1 400–0 m yielded 16 specimens comprising nine species. The species *Lobianchia dofleini*, *Protomyctophum* (*Protomyctophum*) *andriashevi*, and *Scopelopsis multipunctatus*, taken in the latter haul, were not recorded from the shallower hauls. The single N200B haul (day) from 823–0 m yielded one specimen each of *Diogenichthys atlanticus* and *Lampanyctus alatus*, both species being recorded also from the IKMT samples of this cruise.

A haul analysis for the lanternfishes from the South African Museum's IK stations in the region (Grindley & Penrith 1965) is given in Table 6 (IKMT_s). The 26 stations (11 day; 15 night) occupied with the gear during the sampling programme yielded 141 specimens (18 species). Most stations (22) were positioned west of Slangkop (34°09'S 18°19'E). This material was reworked because of errors in identification and nomenclature (see synonymies in Hulley in press). No lanternfish specimens were obtained from the day hauls, fished obliquely to a maximum of 500 m. Myctophids were caught only at five of the night stations, the 82 specimens from the 0–50 m depth strata consisting of a single species, *Lampanyctodes hectoris*. The following species were taken in hauls

TABLE 5
Analysis of myctophid data from MT-1600 net from *Walther Herwig* stations in southern Benguela region.
= number of hauls; SP = number of species; SPP = number of specimens.

Gear Year	#	Total		Time (local)	#	0–112 m		0–305 m		0–592 m		> 1 000 m			
		SP	SPP			#	SP	SPP	#	SP	SPP	#	SP	SPP	
MT-1600 1971	6	46	2 310	0600–1800	1	0	0	0	0	0	0	0	1	17	196
				1800–0600	5	2	28	994	2	34	890	1	28	222	0

TABLE 6
Analysis of myctophid data from various nets deployed in the southern Benguela region.
= number of hauls; SP = number of species; SPP = number of specimens; * = no depth data.

[illegible]

0–200 m and 0–500 m: *Diaphus brachycephalus*, *D. hudsoni*, *D. lucidus*, *D. meadi*, *D. metopoclampus*, *D. mollis*, *D. ostenfeldi*, *Hygophum hanseni*, *H. hygomii*, *Lampanyctus alatus*, *L. australis*, *L. lepidolychnus*, *Lobianchia dofleini*, *Protomyctophum* (*Protomyctophum*) *normani*, *Scopelopsis multipunctatus*, *Symbolophorus barnardi* and *Triphoturus nigrescens*.

Additional lanternfish material in the SAM collections (Table 6: Other) was obtained from 11 hauls occupied with a variety of gear including bottom trawls and N100B nets. Depth data (and in some instances gear type) were not available for eight of these hauls, but the 346 specimens taken by these hauls have been included in Table 6. These specimens comprise the following species: *Diaphus meadi* (1), *Gonichthys barnesi* (293), *Lampanyctodes hectoris* (3), *Lampanyctus lepidolychnus* (1), *Symbolophorus barnardi* (1), and *S. boops* (47). The single species recorded from the two N100B hauls (0–200 m) and the one BT haul (424 m) was *Lampanyctodes hectoris*. During the 1971 transect of FRV *Walther Herwig*, 50 lanternfish specimens were taken at the surface with a David net (Table 6): *Gonichthys barnesi* (42), *Myctophum asperum* (3), *M. nitidulum* (1) and *M. spinosum* (4).

DISCUSSION

Any discussion of distribution in the family Myctophidae should take into account that major ecological differences exist and that parameters affecting distribution patterns in one community may not necessarily be the same in another community. The community structure terminology used in this paper follows Hulley (1981), in which it is suggested that myctophids may be divided into (1) oceanic (= high-oceanic) mesopelagic and bathypelagic communities, and (2) pseudoceanic epibenthic and pelagic communities. However, the groupings within the pseudoceanic zone may not be as distinct. For example, it would appear from the above results that *Lampanyctodes hectoris*, which is at present regarded as a member of the pseudoceanic pelagic community, may be taken in abundance in bottom trawls during the day but may move off the bottom and into the upper 50 m of the water column during the night. A similar behaviour pattern has been reported for the Pacific pseudoceanic species *Diaphus watasei* in Suruga Bay (Kawaguchi & Shimizu 1978). Lanternfish community structure is further complicated by the fact that certain oceanic species, for example *Gymnoscopelus bolini*, *G. braueri*, *G. nicholsi*, *G. piabilis*, *Noto-scopelus kroeyeri*, may be caught (? seasonally) on upper-slope and outer-shelf regions in potentially economic quantities (Dubrovskaya & Makorov 1969; Hulley & Krefft 1985). In addition, other oceanic species (*Diaphus dumerilii*, *Lampanyctus australis*) may possess pseudoceanic populations (Hulley 1981; Rubiés 1985). Comprehensive data on the life histories and reproductive biology of these species is sparse, and more research will be required before delineation of community structure in myctophids can be fully developed.

The interpretation of species complexity and general distribution in this paper is constrained both by a 'division of labour' aspect (i.e. SFRI is

investigating the biology of *Lampanyctodes hectoris*) and by the variety of sampling strategies employed. Depths below 1 000 m were not well sampled (4 daylight hauls), and only 12 pelagic hauls (8 day; 3 night; 1 time unknown) and 6 bottom hauls (all during the day) were made to depths between 500 m and 1 000 m. Therefore, since bathypelagic species are poorly represented in the collections, the main thrust of the discussion will focus on the oceanic mesopelagic community.

The results of the present paper, particularly those from the BT-180 samples, confirm the distinction of at least a pseudo-oceanic lanternfish community and an oceanic community, the former characterized by *Lampanyctodes hectoris*. The data does not allow for closer inspection of the relationships between mesopelagic and bathypelagic species, except to indicate that there may be a degree of depth separation at night (see *Lampanyctus achirus* below). However, penetration of the upper 500 m of the water column by this bathypelagic species does take place in the southern Benguela region.

The physical structure of the seas around South Africa, in particular the South-east Atlantic and Benguela Upwelling Region, has been repeatedly described (see Shannon 1985) and does not need to be given here. Only features that are relevant to the interpretation of the distribution will be discussed.

Firstly, specimens of Indo-Pacific species are advected into the South-east Atlantic in water that originates from the Agulhas Current (Heydorn 1959; Krefft 1974; Weikert 1975; Hulley 1981, 1986; Bekker 1983; De Decker 1984). Thermal infra-red imagery has indicated that at least two mechanisms exist for this advection: (1) the growth, decay and dispersion of shearing eddies on the northern border of the Agulhas Current, with the subsequent advection of fragments into the South Atlantic; and (2) the production of Agulhas Water rings from the Agulhas Current retroflexion area south-west of South Africa (Lutjeharms & Valentine 1981). On the basis of temperature recordings from a satellite-tracked buoy placed in an Agulhas Current fragment, these authors reported that the advected water lost its temperature characteristics (from 17°C to 14°C) over a period of 40 days, owing to mixing with colder South Atlantic water. Although Darbyshire (1966) has suggested that this advected Agulhas Water may be detected as far north as 23°S, its distinction from aged, upwelled Benguela Water at lower latitudes is difficult (Jones 1971). Shannon (1966) has indicated that the advection of this Agulhas Water is at a maximum during summer and autumn, and at a minimum during winter and spring.

Secondly, it would appear that some authors have characterized the offshore region of the eastern South Atlantic, north of the Subtropical Convergence, as subtropical (Boden 1951; Abrams *et al.* 1984; Abrams 1985). However, there is a substantial intrusion of convergence and subantarctic faunal elements into the southern Benguela region and even on to the South African shelf (Krefft 1974, 1978; Hulley 1981; McGinnis 1982; Bekker 1983; De Decker 1984), in association with the north-east deflection of the isotherms and isohalines (D.H.I. *Monatskarten* 1971). Drift-card observations have confirmed the northward flow of surface

water from the Convergence towards the South African coast during the winter months (Shannon *et al.* 1973), while subsurface investigations have demonstrated the existence of a complex cold-core eddy system north of the Convergence to about 31°S (Visser 1969; Shannon & Van Rijswijck 1969; Welsh & Visser 1970; Henry 1975; Lenz 1975; Allanson *et al.* 1981; Lutjeharms & Emery 1983; Lutjeharms *et al.* 1985). These cold-core eddies, which are formed from planetary waves moving along the Convergence becoming unstable and losing their tops, drift northward (Lutjeharms 1981*b*). Although they extend to a depth well below 500 m and can be detected at 1 000 m, they become well mixed with South Atlantic water (Welsh & Visser 1970). This suggests the probability of mixed subtropical–temperate faunas in the study region and the possible existence of a transitional zone similar to that reported off Peru (Parin *et al.* 1973).

Bathypelagic species (Table 7)

Of the five bathypelagic species known from the Atlantic and Indian oceans (*Gymnoscopelus opisthopterus*, *Lampadena anomala*, *Taaningichthys paurolychnus*, *T. bathyphilus*, *Lampanyctus achirus*), only the latter two species should occur in the southern Benguela region (Hulley 1981; Bekker 1983). Isolated specimens of the Antarctic species *Gymnoscopelus opisthopterus* have been taken in trawls fished to below 2 000 m as far north as 40°20'S (Hulley 1981), but sampling at these depths has not yet been undertaken in the southern Benguela region. The deepest haul included in the present survey (WH 417/71) was fished to 1 550 m. One specimen of *Taaningichthys bathyphilus* (58 mm SL) was recorded from 1 000–0 m at 30°19'S 10°08'E. *Lampanyctus achirus* was taken throughout the region (31°19'S–39°06'S and 10°08'E–17°11'E) and, except for a single case, in depths greater than 592 m. However, Hulley (1981) has pointed out that this species may be caught in depths shallower than 500 m in areas of pronounced upwelling, which may account for the record of the specimen (48 mm SL) at 33°44'S 17°11'E from 120 m.

Pseudoceanic species (Table 7)

These are species that are associated with land environments and land-orientated food chains and are distributed on or over continental shelf and slope regions and in the neighbourhood of oceanic islands. On a global basis, the following pseudoceanic species of Myctophidae have been recognized: *Diaphus adenomus*, *D. coeruleus*, *D. garmani*, *D. knappi*, *D. minax*, *D. roei*, *D. sagamiensis*, *D. suborbitalis*, *D. taaningi*, *D. umbroculus*, *D. watasei*, *Idiolychnus urolampus*, *Lampadena pontifex*, *Lampanyctodes hectoris*, and possibly *Diaphus burtoni* and *Myctophum fissunovi* (Krefft 1970; Nafpaktitis & Paxton 1968; Kawaguchi & Shimizu 1978; Nafpaktitis 1978; Hulley 1981; Bekker 1983; Rubiés 1985). Two of these species, *Diaphus garmani* and *Lampanyctodes hectoris*, have been taken in the southern Benguela region. The former species possesses a West tropical Subpattern in the Atlantic (Nafpaktitis *et al.* 1977; Hulley 1981) and in

the Indian Ocean has been recorded from the coast of East Africa, the Comoro Islands, the west coast of Madagascar, off Mozambique, and to about 26°S (Nafpaktitis 1978; Gjøsæter & Beck 1981; Hulley 1984). The single specimen taken during the present surveys, at 33°34'S 17°32'E (bottom depth 404 m), represents the first record of *Diaphus garmani* in the eastern South Atlantic. Its presence here appears to be associated with the advection of Agulhas Water into the region rather than an association with the bottom depth. An additional record at 36°33'S 20°01'E serves to link the distribution to that in the Agulhas Current. *Diaphus taaningi* is known from the Mauritanian Upwelling Region, Gulf of Guinea, and south to about 24°S (O'Toole 1976; Hulley 1981; Rubiés 1985; SAM data), while *Lampadena pontifex* has been caught at 24°26'S 13°30'E (Karrer 1975), between 23°30'S 12°45'E and 25°30'S 12°27'E (SAM data), and 'sporadically' to about 28°30'S (Rubiés 1985). These records suggest that the two species might be expected within the southern Benguela region as defined here.

Oceanic species (Table 7)

In addition to the four bathypelagic and pseudoceanic species, 61 oceanic mesopelagic species of Myctophidae were taken during the sampling in the southern Benguela region. These are listed in Table 7, which is based on the Atlantic Ocean distribution patterns and subpatterns given by Hulley (1981).

Bekker (1983) recorded the following species from the region, but no specimens of these were taken during the sampling cruises of the present survey: *Bolinichthys photothorax*, *Diaphus holti*, *D. termophilus*, *D. problematicus*, *Electrona antarctica*, *Gonichthys venetus*, *Gymnoscopelus fraseri*, *G. braueri*, *Lampadena dea*, *L. chavesi*, *L. urophaos*, *Myctophum obtusirostre*, *Taaningichthys miminus*. However, recent investigations indicate that *Diaphus holti*, *Lampadena dea* and *L. chavesi* are known from off the South West African–Namibian coast (Rubiés 1985).

Species that have a Broadly Tropical distribution pattern in the Indian Ocean (*Diaphus parri*, *D. richardsoni*, *Diogenichthys panurgus*, *Lampanyctus turneri*, *Myctophum spinosum*, *Triphoturus nigrescens*) manifest themselves in the Agulhas Subpattern of the Atlantic Ocean. These species, together with *Diaphus diadematus* (Extended Agulhas Subpattern), are advected in Agulhas Water pockets into the southern Benguela region and also, in the case of the latter species, may be associated with aged upwelled Benguela Water. None of these species was recorded by Rubiés (1985) off the South West African–Namibian coast. In a similar manner, Atlantic holotropical species (*Bolinichthys supralateralis*, *Diaphus luetkeni*, *Lampanyctus nobilis*)—which are more widely distributed in the Indo-West Pacific—thermophilic-eurytropical species (*Diaphus brachycephalus*, *D. lucidus*, *D. perspicillatus*, *D. splendidus*, *Myctophum nitidulum*), and possibly certain holoeurytropical species (*Myctophum selenops*), penetrate the southern Benguela region with Agulhas Water.

TABLE 7

Analysis of myctophid data from all types of gear. Distributional patterns and subpatterns after Hulley (1981).

<i>Pattern</i>	<i>Subpattern</i>	<i>Species</i>	<i>No. specimens</i>	<i>SFSA No.</i>
OCEANIC BATHYPELAGIC				
Widespread Temperate	South Temperate Subantarctic	<i>Taaningichthys bathyphilus</i>	1	86.123
		<i>Lampanyctus achirus</i>	45	86.73
PSEUDOCEANIC PELAGIC				
Tropical Benguela	West Tropical	<i>Diaphus garmani</i>	1	86.19
		<i>Lampanyctodes hectoris</i>	> 10 842	86.72
OCEANIC MESOPELAGIC				
Widespread		<i>Diogenichthys atlanticus</i>	144	86.42
		<i>Electrona risso</i>	18	86.47
		<i>Lobianchia dofleini</i>	391	86.92
		<i>Notolychnus valdiviae</i>	69	86.106
Broadly Tropical	Holoeurytropical	<i>Ceratoscopelus warmingii</i>	366	86.9
		<i>Diaphus mollis</i>	46	86.28
		<i>Lampanyctus photonotus</i>	3	86.83
		<i>Lobianchia gemellarii</i>	33	86.93
		<i>Myctophum selenops</i>	4	86.104
		<i>Notoscopelus resplendens</i>	124	86.108
	Thermophilic- eurytropical	<i>Diaphus brachycephalus</i>	7	86.13
		<i>Diaphus lucidus</i>	71	86.23
		<i>Diaphus perspicillatus</i>	11	86.32
		<i>Diaphus splendidus</i>	2	86.37
		<i>Myctophum nitidulum</i>	2	86.101
	Thermophobic- eurytropical	<i>Benthoosema suborbitale</i>	102	86.3
		<i>Lampanyctus alatus</i>	155	86.74
		<i>Lampanyctus lineatus</i>	1	86.80
	Agulhas	<i>Diaphus parri</i>	3	86.31
		<i>Diaphus richardsoni</i>	2	86.35
		<i>Diogenichthys panurgus</i>	1	86.43
		<i>Lampanyctus turneri</i>	13	86.87
		<i>Myctophum spinosum</i>	4	86.105
		<i>Triphoturus nigrescens</i>	6	86.125
	Extended Agulhas	<i>Diaphus diadematus</i>	96	86.14
Tropical	Holotropical	<i>Bolinichthys supralateralis</i>	5	86.7
		<i>Diaphus luetkeni</i>	3	86.24
		<i>Lampanyctus nobilis</i>	2	86.82
		<i>Myctophum asperum</i>	3	86.98

OCEANIC

MESOPELAGIC (*contd*)

Subtropical	Bisubtropical	<i>Bolinichthys indicus</i>	20	86.4
		<i>Diaphus effulgens</i>	14	86.16
		<i>Diaphus metopoclampus</i>	46	86.27
		<i>Hygophum hygomii</i>	179	86.61
		<i>Lampanyctus ater</i>	55	86.75
		<i>Lampanyctus festivus</i>	33	86.77
		<i>Lampanyctus pusillus</i>	306	86.84
	South subtropical	<i>Myctophum phengodes</i>	23	86.103
		<i>Scopelopsis multipunctatus</i>	172	86.118
		<i>Symbolophorus barnardi</i>	162	86.119
Temperate	Bitemperate	<i>Lampadena speculigera</i>	12	86.71
		<i>Lampanyctus intricarius</i>	9	86.78
		<i>Lampanyctus macdonaldi</i>	1	86.81
		<i>Loweina interrupta</i>	1	86.94
	South temperate Convergence	<i>Diaphus meadi</i>	1 436	86.26
		<i>Diaphus ostensfeldi</i>	15	86.30
		<i>Gonichthys barnesi</i>	335	86.49
		<i>Hygophum hanseni</i>	22	86.60
		<i>Lampadena notialis</i>	22	86.69
		<i>Lampanyctus australis</i>	420	86.76
		<i>Lampanyctus lepidolichnus</i>	278	86.79
		<i>Lampanyctus</i> sp. B	9	86.89
		<i>Lampichthys procerus</i>	287	86.90
		<i>Protomyctophum normani</i>	4	86.116
		<i>Protomyctophum subparallelum</i>	11	86.110
	Subantarctic holosubantarctic	<i>Electrona carlsbergi</i>	2	86.45
		<i>Protomyctophum andriashevi</i>	1	86.111
		<i>Protomyctophum parallelum</i>	1	86.109
	Subantarctic semisubantarctic	<i>Diaphus hudsoni</i>	472	86.20
		<i>Gymnoscopelus piabilis</i>	8	86.58
		<i>Metelectrona ventralis</i>	45	86.96
		<i>Symbolophorus boops</i>	316	86.120

Table 8 gives catch rates for each of the pattern types on the basis of four cruises, during which RMT-2 (PAUG82), RMT-8 (PAUG83, PAUG84), and MT-1600 (WH-71) nets were deployed. The percentage contribution for each of the patterns and subpatterns, based on the mean catch rate (specimens per 1 000 m³) is given in Figure 2.

Catch rates for the Thermophilic-eurytropical, Agulhas, Extended Agulhas and Holotropical subpatterns are low (Table 8), suggesting that all of the above species show a 'tailing' distribution (i.e. a decline in density with increasing latitude—see Hulley 1981, figs 39, 56, 67, 95) in the Agulhas Current, with a correlated low abundance value in the eastern South Atlantic. It should be noted that specimens of *Myctophum asperum*, *M. nitidulum* and *M. spinosum* were taken at the surface during sampling with a David net. The seasonality of occurrence of such species in this region will be examined in a later paper.

TABLE 8

Catch rates, percentage contribution and stock estimate for oceanic mesopelagic species of Myctophidae from SFRI Phyllosoma Surveys and from *Walther Herwig* stations in the southern Benguela region. Patterns and subpatterns after Hulley (1981).

Pattern	Subpattern	Catch rate (specimens/1 000 m ³)			Mean	%
		PAUG82 RMT-2	PAUG83/84 RMT-8	WH-71 MT-1600		
Widespread		0,3188	0,0372	0,1192	0,1586	9,67
Broadly Tropical	Holoeurytropical	0,1889	0,2079	0,0599	0,1522	9,28
	Thermophilic-eurytropical	0,0202	0,0124	0,0216	0,0181	1,10
	Thermophobic-eurytropical	0,2986	0,0365	0,0035	0,1129	6,88
	Agulhas	0,0101	0,0022	0,0041	0,0055	0,34
	Extended Agulhas	0,0186	0,0080	0,0261	0,0176	1,07
Tropical	Holotropical	0,0034	0,0022	0,0009	0,0022	0,13
Subtropical	Bisubtropical	0,3876	0,0496	0,0968	0,1780	10,85
	South subtropical	0,3475	0,0285	0,0285	0,1348	8,22
Temperate	Bitemperate	0,0219	0,0015	0,0017	0,0084	0,51
	South Temperate (Convergence)	0,9144	0,4676	0,3548	0,5789	35,29
	Subantarctic (Holosubantarctic)	0,0000	0,0000	0,0007	0,0002	0,01
	Subantarctic (Semisubantarctic)	0,6866	0,1160	0,0163	0,2730	16,64
Gear catch rate		3,2166	0,9696	0,7341		
Mean specimen weight (g)		0,2	0,5	1,0		
Stock estimate (tonnes)		10 × 10 ⁶	8 × 10 ⁶	12 × 10 ⁶		

As pointed out above, the hydrography of the southern Benguela region offshore of the continental shelf break suggests that in the main there should be a mixed temperate-subtropical mesopelagic fauna. The results indicate that this is true and that temperate species (52%) and subtropical species (19%) comprise about 71 per cent of the total lanternfish fauna. The compositional value for the broadly tropical element—i.e. those species distributed in both tropical and subtropical waters—approximates that of the subtropical element, while widespread species comprise about 10 per cent of the myctophid fauna.

All Atlantic widespread species are found in the southern Benguela region, namely *Diogenichthys atlanticus*, *Electrona risso*, *Lobianchia dofleini* and *Notolychnus valdiviae*. The Warm Water Group, which comprises about 37 per cent of the fauna, includes Holoeurytropical, Thermophobic-eurytropical, Bisubtropical and South subtropical Subpattern species. The percentage contribution of each of these subpatterns to the myctophid fauna ranges between 7 and 11 per cent (Fig. 2). Of the 12 holoeurytropical species known from the Atlantic Ocean, six species (*Centrobranchus nigroocellatus*, *Diaphus subtilis*, *Gonichthys cocco*, *Hygophum reinhardtii*, *Loweina rara*, *Notoscopelus caudispinosus*) have not been recorded in the southern Benguela region. *Lampadena chavesi* and

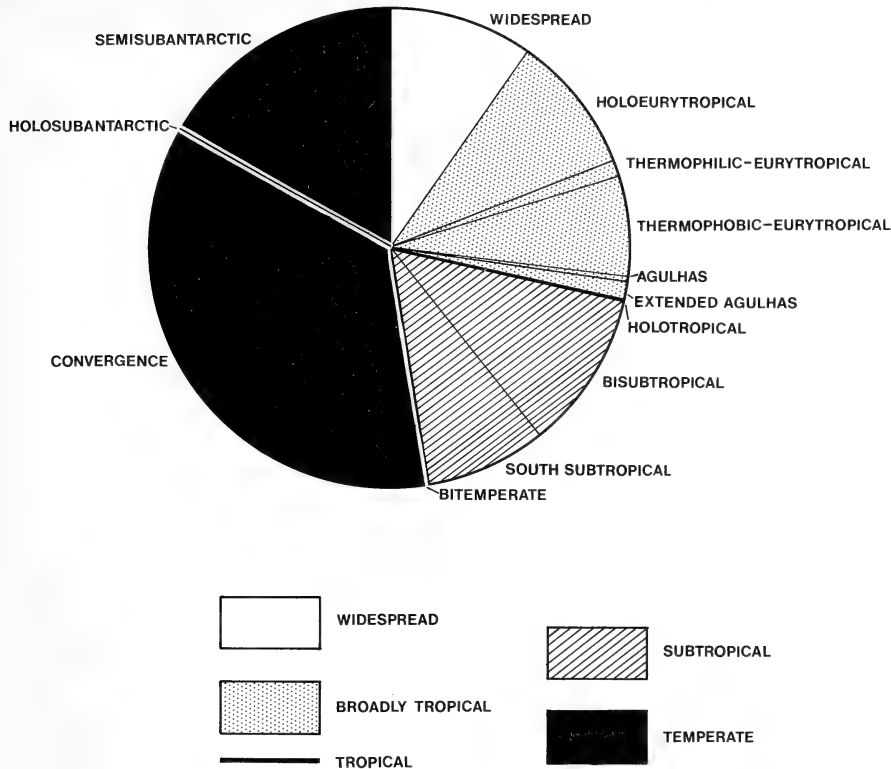


Fig. 2. Percentage composition by pattern and subpattern of high-oceanic species of Myctophidae, based on catch rates of RMT-2, RMT-8 and MT-1600 nets from SFRI Phyllosoma Surveys and from *Walther Herwig* stations in the southern Benguela region.

Taaningichthys minimus (Bisubtropical Subpattern: 9 Atlantic species) and *Diaphus anderseni* (South subtropical Subpattern: 4 Atlantic species) have also not been recorded. All Thermophobic-eurytropical Subpattern species known from the Atlantic have been taken in the region. The somewhat low percentage contribution of species of this subpattern is difficult to interpret at this stage; it may be due either to a sampling artifact or related to the small number of species involved (*Lampanyctus lineatus* is an uncommon species with a night distribution at 150–350 m and 900–1 000 m—Nafpaktitis *et al.* 1977), or both.

Cool Water Group temperate species, which comprise about 52 per cent of the myctophid fauna in the southern Benguela region, include bitemperate (<1%), convergence (35%), semisubantarctic (17%), and holosubantarctic (<1%) species (Table 8). This confirms the strong intrusion of southern elements into the southern Benguela region, particularly those species associated with the Subtropical Convergence and with the region between the Convergence and the Subantarctic Divergence, and agrees with the conceptual image of the region

derived from physical studies. Whether this compositional structure changes with decreasing latitude is difficult to assess, since comparative data are not given by Rubiés (1985) for the South West African–Namibian myctophids. However, he has pointed out (p. 581) that most are subtropical species and that ‘subantarctic’ species, i.e. ‘coming from the Convergence area’, were caught in very small numbers.

Stock estimate

Mean catch rates for each subpattern (specimens/1 000 m³) for the PAUG82 (RMT–2), PAUG83 and PAUG84 (RMT–8) and WH–71 (MT–1600) cruises have been calculated from abundance values (specimens/hour). These are presented in Table 8. Estimates of the stock of lanternfishes in the offshore area of the eastern South Atlantic are calculated as 10×10^6 tonnes in the case of sampling with an RMT–2; 8×10^6 tonnes with an RMT–8; and 12×10^6 tonnes with an MT–1600 net. The mean value (10×10^6 tonnes) represents about 62 per cent of the abundance estimate for mesopelagic fishes of the South-east Atlantic (Gjøsaeter & Kawaguchi 1980) and compares with the lanternfish composition by number (56%) for Transect II of the 1971 cruise of FRV *Walther Herwig* (Hulley 1981). However, this transect also encompassed subtropical and tropical regions. Since Hulley & Krefft (1985) have demonstrated that smaller populations of myctophids occur in warm-water species than in cold-water species, the mean stock estimate of 10×10^6 tonnes appears to be realistic.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Capital initial letters

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e.g. '... the Figure depicting *C. namacolus* ...': '... in *C. namacolus* (Fig. 10) ...'
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FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74** (33): 627–634.

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THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

(continued inside back cover)

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OF THE KHOISAN

By
M. L. WILSON

Cape Town Kaapstad

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[MS accepted 10 April 1986]

ABSTRACT

The origin, meaning and use of the various names and terms applied to the indigenous non-Negro peoples of southern Africa are discussed. It is concluded that, while the various other branches of anthropology should use a common set of names or terms, archaeologists should, in general, restrict themselves to the use of terms such as 'herder' and 'hunter-gatherer'.

CONTENTS

	PAGE
Introduction	251
Khoikhoi	252
San	254
Hottentot	256
Bushman	257
Khoisan	259
Herders and hunters	260
Discussion and conclusions	261
Acknowledgements	264
References	264

INTRODUCTION

*What's in a name? that which we call a rose
By any other name would smell as sweet.*

Shakespeare: *Romeo and Juliet*

During the 1971 conference on 'The Peoples of Southern Africa', sponsored by the Royal Society of South Africa and the South African Institute for Medical Research, a session was devoted to nomenclature. The majority of the participants agreed to the adoption of a tripartite terminology to cover the three main areas of research. Excluding the terminology for the Negroes, which is not relevant here, the consensus was that 'San' and 'Khoikhoi' should be applied to biological entities; 'Bushman' and 'Hottentot' to languages; and 'hunters' or 'hunter-gatherers' and 'herders' or 'pastoralists' to economy or way of life (Jenkins & Tobias 1977: 51). These names or terms provide suitable headings for discussion although it is not always possible to keep them entirely separate. The term 'Khoisan' is included since it is also in current use.

KHOIKHOI

The first recorded use of a cognate of this name is in the entry of 9 January 1653 in the journal of Jan van Riebeeck, where it is rendered as *Quena* (Thom 1952: 127). The name was, however, not commonly used and did not gain currency among the early settlers and travellers.

Nienaber (1963: 310–311, 378–380, 384–385) lists, among others, the following early usages and their attributed meanings: Witsen, 1691, *quena*, the Hottentot nation, *k'quique*, a man; Valentyn, 1705, *t-hoekoe* and *thóekoe*, a Hottentot, *quoique*, a man; Kolb(en), 1708, *q~ena*, the Hottentot nation, *q~uoique*, a man; Thunberg, 1773, *Keuna*, people; Le Vaillant, 1780–83, *khoé-khoep*, Hottentot man; Von Winkelmann, 1788, *xkeukoe*, (the) people; Barrow, 1797, *Quaiquae*, the name 'by which the whole nation was distinguished, and which at this moment they bear among themselves in every part of the country', *quaina*, man. (The dates given by Nienaber refer to the observation, not to the publication.) To these may be added the observation by Robert Jacob Gordon, who died in 1795 and was probably the most widely travelled man up to that time, that *Queuna* was the plural of *Quoi*, person (Forbes in Sparrman 1975: 181 n23). More recently, Stow (1905: 31) commented that: 'These people, who were severally known to the old colonists and early writers as the Bosjesmans, the Boschimans, and Bushmen, appear to have adopted among themselves the name of 'Khuai, which is also the same as that given to the natural apron for which the women of pure Bushman and Hottentot races are distinguished; and it was thus probable that the appellation 'Quae-'quae, or perhaps more properly 'Khuai-'Khuai or 'Khuai-'quae—the people of the Apron, was derived.' Stow's comment is of interest in that he applied the name to Bushmen, whereas it is generally taken to have been the name of the Hottentots. Schapera (1930: 428) gave the Naron (= Nharo, one of the 'Hottentot' languages) *kwellkwa*, men, and *kwene*, people, and the Nama *khoii*, person, and *khoïn*, people. Kroenlein's Nama dictionary gives 'Khoi-khoïn' as meaning *die Naman*, the Nama (Rust 1969: 238).

According to Nienaber (1963) these names represent dialectal variants, those given by Witsen, Kolb and Valentyn being in the 'Cape' dialect, the others in his list being 'Eastern'. Schapera's and Kroenlein's should be 'Northern', but according to Nienaber's classification Gordon's *Queuna* (Forbes in Sparrman 1975) could be either 'Cape' (cf. Witsen and Kolb above) or 'Eastern' (cf. Thunberg and Barrow above), while Stow's (1905) seem closer to the latter.

Nienaber (1963: 311) observed that when the language became more normalized the name was written *Khói-khói-n* in Nama and, according to Meinhof, *khoë-khoe-n-a* in Korana, both with the meaning 'Hottentots'. This is based on the (masculine) singular *khoi-b*, man or person, which in reduplicative apposition became the people's name, meaning 'the people of people', or 'the real (or "true") people'. Nienaber does not cite a source for this translation, but Nienaber & Raper (1977: 31) cite the missionary Knudsen as having recorded in 1842 that 'Khoi-khoïn' meant '*Mensch-Menschen oder Mensch der Menschen*'. The literal translation of these, 'person-people' and 'person of the people' (or

even 'of humankind'), is awkward. The second of Nienaber's translations is more suitable—better yet that of Hahn (1881: 2), 'men of men, i.e. men *par excellence*'. It seems legitimate to wonder whether these translations are semantically correct, particularly in view of the wide range of early meanings given above, and perhaps more specifically with regard to the meaning attributed to the Nharo *kwellkwa*. If the translations of Knudsen and others (Hahn was the son of a missionary) were no more than pious attempts to uplift the people from the degradation into which they had fallen (or been thrust), after more than a century of these meanings being applied it is probable that today no Nama would know differently. W. H. G. Haacke, a linguist researching the Nama language and one of the contributors to a new Nama dictionary currently being compiled, considers Hahn's translation to be dubious, but says that further research is needed (1985 pers. comm.).

In the current orthography for the Nama–Damara language accepted by the South West African Department of Bantu Education (1977: 29) it is laid down that: 'All words which in the past were spelt with the letters *-oi-* are spelt with *-oe-* in the standardised orthography. . . .' Haacke (1982: 78) commented that 'Khoi-khoi' is antiquated and used instead 'Khöëkhöë'. Haacke (1985 *in litt.* and pers. comm.) has pointed out that Nama has no sound corresponding to the *-oi-* diphthong. The two vowels were originally separated by a now-elided consonant (probably *-w-*), and are pronounced separately and are different tonally. Approximate phonetic equivalents are as in 'port' and 'fare' (International Phonetic Alphabet symbols ɔ and eə).

What is important is whether, however the name is spelt, this Nama dialectal variant can properly be applied to all the people, past and present, to whom it refers. The now-extinct speakers of the 'Cape' dialect seem to have called themselves *Khoina* or something similar and it does not seem proper to call these people by a name they would not have called themselves. However, if the oral traditions of the Korana (Engelbrecht 1936: 2 ff.) are correct in asserting that they, or some of their number, earlier lived closer to the Cape (i.e. modern Cape Town), then it is arguable that 'Khoekhoe' (omitting the tonal marks, as will inevitably happen if this word is accepted) may be a modern variant of an earlier 'Cape' dialectal form. Whether or not 'Khoina' and 'Khoekhoe' had or have the same meaning is a matter for linguists to determine. It seems unlikely, however, that the Nama would have two words, *Khoen* and *Khoekhoen*, with precisely the same meaning, 'people'.

Two historians, Böeseken and Elphick, conducted a scholarly debate for some years on the meaning, origin and use of 'Khoikhoi', 'San' and 'Khoisan' (Böeseken 1972, 1974, 1975; Elphick 1974, 1975). The arguments on both sides are persuasive but in the end one is obliged to agree with Böeseken that there is no documentary evidence from the historical period for the common use of 'Khoikhoi' (or its cognates) as a generic by the people themselves.

G. Klinghardt (1985 pers. comm.) has pointed out that, in considering the various names, it is important to bear in mind the different levels of identity on

which a person can operate. These can range from: individual; member of a smaller group (e.g. clan); member of a larger group (e.g. tribe); to member of the largest group (e.g. nation, humankind, or all those who are considered to be 'the same'). He has also drawn attention to the fact that in the historical records there is little indication that the Khoikhoi had a sense of nationhood, the tribe usually being the largest cohesive unit (see also Elphick 1985: 68). The possibility thus exists that, while 'Khoikhoi' may have been understood as a generic ('us', as distinct from 'them'), it may simply have been a general term for 'people'.

Orthographically, the apocopic use of 'Khoikhoi' or 'Khoekhoe' without the gender: number suffix, and perhaps also the omission of the tonal marks, should not be condoned; and the use of the abbreviated forms, 'Khoi' and 'Kho', is even less excusable. Nienaber (1985 *in litt.*) has pointed out that 'Kho' simply means 'person'. Haacke (1985 *in litt.*) has, however, suggested that because of the possibility of confusion or error—there are different suffixes for masculine, feminine, singular, plural, dual and common plural—it is perhaps preferable to drop the suffix unless actually writing the language.

A point that is less frivolous than it may seem is that, while the replacement of the long-ingrained 'Khoikhoi' by 'Khoekhoe' may cause little concern to serious anthropologists, the introduction of this word into the 'popular' literature without any indication of its correct pronunciation, and which so resembles the Afrikaans 'koekoek' and its English counterpart 'cuckoo', is liable to bring it into the same sort of disrepute as that into which 'Hottentot' is said to have fallen (e.g. Wilson 1969: 40). It was not serious researchers who degraded 'Hottentot' but the ignorant and uninformed or, following Elphick (1985: xv), 'the intellectual climate of eighteenth-century Europe'.

The questions to be answered in this regard are, then, whether 'Khoikhoi' or 'Khoekhoe' were ever commonly used by the people as a (generic) name for themselves; whether what appears to be a dialectal form is correctly applicable to *all* the people, some of whom may have used another form; and whether 'Khoekhoe' is not liable to bring the name into derision. The actual, or original, meaning of the name may be of lesser importance, especially as there is no evidence of any derogatory connotation.

SAN

The first recorded use of a cognate of the name 'San' is the same as that for *Quena* given above, where it is written *Soaqua* and applied to the elusive *Visman* ('Fishermen' or perhaps just 'Fishmen') by the 'Saldanhars' (at that time 'Hottentots' *sensu lato*) (Thom 1952: 127). Unlike *Quena*, however, the name occurs fairly frequently in various forms in the records of the second half of the seventeenth century (see, for example, references under 'Soaqua' in the index of Moodie 1960a-c).

Hahn (1881: 3), while admitting that the meaning of the Nama word *Sān* was not quite intelligible, traced its origin to the root *sā*, which he interpreted as

meaning 'aborigines' or 'settlers proper'. However, in the vocabulary of Hottentot and Bushman words he provided, Hahn (1881: 7) gave the Hottentot *sāb* and Bushman *tsā* as meaning 'buchu'. Smith (1966: 165–166), a botanist, suggested that 'Sab', plural 'San', meant 'bushes' and that the name was applied because the people so called used the aromatic leaves of the buchu plant (see Smith 1966: 135–141 under 'boegoe' for discussion of the wide range of species to which the name has been applied). Westphal (1971: 369) translated the root *sā* as meaning 'gather food'. However, Nienaber (1985 *in litt.*) is of the opinion that the various translations are 'oogfilologies'—based on the visual similarities of words—and fortuitous. It thus seems likely that the ascription by Elphick (1977: 27–28, 1985: 27–28) of a 'San' suffix to the names of various tribes, such as Horisans, Cochesons and Kamesons, may be equally fortuitous. (The early records are not clear as to the identities of these peoples. For example, in the only two references to the Kamesons, the journal of Van der Stel's expedition to Namaqualand (Moodie 1960a: 409–410) records that 'we found among the Amaquas several of those Hottentots who are called *Kamesons*'. Later, members of the party happened upon a group of five men, who were called 'Sonquas', one of whom was captured and taken back to Van der Stel and 'the Commander sounded the Sonqua, who now said he was no Sonqua, but one of the tribe called *Kamesons*'. From this, it seems not improbable that the early settlers and travellers termed 'Sonquas' any people they found without domestic stock; though in this case the party that captured the so-called 'Sonqua' included four of the expedition's Hottentots, who ought to have recognized him as one of their own kind, if, in fact, he was. G. Klinghardt (1986 pers. comm.) is of the opinion that the man was a !Gami-≠nun (Bondelzwart, one of the major divisions of the Nama) and that the 'Sonqua' with whom he was living were clients of the 'Amaquas' (= Nama) in that area.)

Haacke (1985 pers. comm.) has mentioned that there are tonal differences in the pronunciation of the two words and that it is thus doubtful that *Sān*, 'Bushmen', derives from *sā*, 'gather'. He has also pointed out that if the gender: number suffix is to be dropped from 'Khoekhoe', for the sake of conformity this should also be done with 'San': thus, *Sā*, or in the new Nama orthography, *Sàà*.

In the early records the use of this name or its variants is often coupled with some pejorative comment, though it is sometimes also used neutrally, as an identifier. Examples of the former are 'Soanqua who are robbers, and are enemies to them and all the Saldanhars' (Thom 1954: 49); 'Souquas or bandits' (Thom 1958: 24); 'It is from the Soncquas that we have to expect the greatest mischief towards the burgers. A people of this sort called Obicquas . . . took the cattle of a party of burgers . . . and killed one of the party. . . . These are a kind of men who live in the mountains, who maintain themselves entirely by robbery, and have nothing to lose by war; they do not hesitate, upon a favourable opportunity, to steal the cattle of their own nation, under whose dominion they live, and therefore the [Hottentot] Captains are always looking out for

opportunities for revenge' (Moodie 1960a: 392). Examples of neutral usage are 'the Souquas (the hill people, who subsist chiefly by the game they kill)' and 'we found no Souquas here' (Moodie 1960a: 225, 231).

Hahn (1881: 3) commented: 'The word *sā(b)* has also acquired a low meaning and is not considered very complimentary. The Khoikhoi speak of *!Uri-Sān* (white Bushmen) and mean the low white vagabonds and runaway sailors who visit their country as traders. One also often hears "*Khoikhoi tamab, Sāb kē*", he is no Khoikhoi, he is a Sā, which means to say, "*he is no gentleman, he is of low extraction, or he is a rascal*"' (Hahn's emphasis). Elsewhere Hahn (1881: 101) noted that the Nama called others of their kind 'Bushmen', 'especially when they are servants, or if they lead a Bushman's life, and have no cattle and sheep'.

Lee (1979: 29–30), commented that 'these Southern African peoples [Bushmen and Hottentots] were tagged with names not of their own choosing that bore little or no relation to the names they used for themselves. Further, such names often had derogatory or racist connotations.' He was none the less content to accept the use of 'San', which he described as 'a comparatively neutral term originally applied by the Khoi-khoi to their hunting and gathering neighbours'. This was in spite of his further observations that 'even San is not an entirely satisfactory term. First, it too has a derogatory connotation, meaning "a rascal" in Khoi-khoi. Second, because of the tremendous linguistic diversity among the Kalahari San of today, over a dozen self-applied terms are in use by various peoples, and San is not one of them!' Lee's unacknowledged source of the connotation was probably Hahn (1881: 3), perhaps by way of Dornan (1925: 43); and in the nineteenth century 'rascal' had a much stronger force than the somewhat jocular connotation that attaches to it today. Lee's attempt to justify the use of the name, despite its not being the people's own name for themselves and its having a derogatory connotation, is as unacceptable as his defence of the use of '!Kung' in place of the name the people use for themselves: '!Kung is easier to pronounce than *žu''hoasi*' (Lee 1979: 31).

The evidence is thus that 'San', of which the meaning is not known, is not, and apparently never has been, the peoples' own name for themselves (but see the observations by Burchell (1967a) and Smith (1830) under 'Bushmen', pp. 258–259) and, however much it might have been accepted by anthropologists, it has, and apparently always has had, a derogatory connotation. Its use should not therefore be condoned, but the problem is to find an acceptable alternative.

HOTTENTOT

In 1620 De Beaulieu wrote of the people met on the shores of Table Bay: 'Their usual greeting on meeting us is to dance a song, of which the beginning, the middle, and the end is *hautitou*' (Raven-Hart 1967: 101). In 1623 Olafsson repeated a similar tale, but used the word 'Hottentott' (Raven-Hart 1967: 112). In 1627 Herbert called the people 'Hatten-totes' (Raven-Hart 1967: 119) and in 1640

De Graaf applied to them the name by which they were to become known in the succeeding centuries, 'Hottentots' (Raven-Hart 1967: 154).

Although this name (or a variant of it: Bosman & Thom (1952: 20) gave 'Ottento', Thom (1952: 21) 'Hottentot' and Moodie (1960a: 9) 'Ottentoo') was first recorded by the white settlers on 7 April 1652, the use of other names such as 'Saldanhars' or 'Strandloopers' was almost more common. Later, as the names of the tribes became known, these were generally used; but the name 'Hottentot' was commonly used as a sort of generic for all the (non-Negro) peoples with whom the settlers and early travellers came into contact. This included people who would now be classified as 'San', for example, 'Some Hottentots of the Obiqua tribe' (Moodie 1960a: 391) and 'Sonquase Hottentots' (Schrijver, 1689, *in* Mossop 1931: 226). The name has also been applied to the Gonaqua of the eastern Cape, who had a long history of interbreeding with their Negro neighbours, the Xhosa (Masson 1776: 284-296; Soga 1930: 94-95; Maingard 1931: 500-501, 504; Harinck 1969: 153-159).

Objections to the use of 'Hottentot' are that it is not the people's name for themselves and that it has acquired derogatory connotations (Wilson 1969: 40; Elphick 1977: xv, 1985: xv; Lee 1979: 29; etc.). Against the first objection it can be argued that 'American' is not an indigenous name; that the name 'Indian', as applied to the indigenous inhabitants of North and South America, is neither indigenous nor correct; that 'English' is correctly applicable to only some of the inhabitants of England; and that the 'Germans' do not call themselves by that name when speaking their own language. What matters, surely, is whether any name is acceptable to the people to whom it is applied. Against the second objection there can be little argument, although Nienaber & Raper (1977: 33) have observed that the name 'Hottentot' is used by the people themselves, and without a sense of derogation. However, G. Klinghardt (1985 pers. comm.), who has carried out research in Namaqualand, has mentioned that the name 'Hotnot' is generally applied to persons considered to be of lower status and never to oneself or to equals except humorously. 'Hottentot' is applied specifically to the offspring of Nama and Dama parents.

Where reference is made to 'Hottentots' in the early records or the literature, it is not always possible to be sure that this term can be replaced by 'Khoikhoi' or some other preferred term, and in these cases the name should be retained. The pros and cons of the use of 'Hottentot' and 'Khoekhoen' are discussed more fully by Nienaber & Raper (1977: 29-34). The conclusion seems to be that there are cases where the retention of 'Hottentot' is justified, others where it is not.

BUSHMAN

This name was first recorded in 1682 by Bergh (*in* Mossop 1931: 85) with reference to people met along the Berg River: 'We came to some Hottentots, they being Somquaas alias Bushmen.' In the entry in the Company's journal for 31 October 1685 (see Elphick (1972: 58) for correction of the date given by

Moodie) there is a reference to 'Sonquas, commonly called Bosjesmans' (Moodie 1960a: 399, under Oct. 3). However, despite the assertion that the Sonqua were commonly called Bosjesmans, there is little evidence of this during the remainder of the seventeenth century, it still being more usual to write of 'Sonquas', 'Obiquas' or variants of these (e.g. Moodie 1960a: 400-446). In the early part of the following century Kolb mentions the 'Odiquas' and 'Sonquas' as well as, but apparently distinct from them, 'a Sort of *Hottentot Banditti* . . . called Buschies or Highway Men' (Kolb 1738: 63, 75-77, 90—Kolb's emphasis). These last were, in Kolb's view, Hottentots who had become renegades and robbers, 'finding the Laws and Customs of their Countries to be too great Restraints upon their Inclinations', and not a separate race. Valentyn (1973: 60), who visited the Cape between 1685 and 1714, merely lists the 'Sonquaas' among the Hottentot tribes, although his transcription of Starrenburg's journal (Valentyn 1973: 20) does include the name 'Bosjesmans'.

By 1770 the official documents tended to use the term 'Bosjesmans' or, in translation, 'Bushmen' (e.g. Moodie 1960b: 3, 11). In 1775 Sparrman (1975: 194) commented that 'There is another species of Hottentots, who have got the name of *Boshies-men*, from dwelling in woody or mountainous places' (Sparrman's emphasis). This suggests that by this time the opinion that the two groups were different had not yet been formalized. Indeed, in 1779 Field Sergeant Charl Marais recorded the allocation to his men of a number of 'little Bushmen' who had been captured, comprising 'a girl . . . a Hottentot . . . a Hottentot . . . a little Hottentot . . . a girl . . . a little boy' (Moodie 1960b: 81).

In 1809 Colonel Collins (Moodie 1960c: 2 ff.) referred to the 'Bosjesmen' without any suggestion that they were a part of the 'Hottentot nation'. However, in 1811 Burchell (1967a: 64) commented on the name 'Bushman' that 'This is often written Bosjesman, and Buschman, which merely being Dutch words signifying men living wild among the bushes, and applied generally to several tribes of the Hottentot race, I have preferred using the English orthography, viewing it rather as a descriptive, than as a proper, name. They call themselves *Sáqua*; those, at least, who inhabit the country southward of the Gariép [Orange River]. Yet it is difficult to avoid inaccuracy, in the application of one collective name to a race of people who divide themselves into so many separate tribes.'

Smith (1830: 171-175, 179) asserted that: 'The Aborigines of South Africa . . . will be found to have consisted, and still to consist, only of two distinct races, namely those of the Hottentot and Caffer. . . . Among these, one division has always held, and still continue to hold, a most conspicuous position, and has ever been proverbial with the rest, on account of its troublesome character and universally outrageous conduct. To this the other tribes, as well as its own member[s], apply the name of *Saap* or *Saan*, and history describes a portion thereof under the appellation of Bushmen. . . . The majority of the Bushmen [*sic*] population, according to the restricted sense in which the term is here to be understood, consists of pure Hottentots; and the remainder of blacks either the offspring of an intercourse with the former and other coloured persons, or else

the actual outcasts of other races themselves. . . . The Hottentot Bushman presents most of the physical characters of the race as exemplified in other situations, and the mixed description according to circumstances, exhibits more or less of the appearances of the Negro or Caffer. . . . The language spoken by the Bushmen, is decidedly a dialect or dialects of that in use by the Hottentots elsewhere; but in most situations is so altered and modified, as that its origin and dependance [*sic*] can scarcely be traced.'

Smith's opinions were probably representative of the majority of 'scientific' opinion during the nineteenth century, i.e. that the Bushmen were biologically Hottentots or of mixed race. However, towards the end of the century Stow (1905: 11) suggested 'that both Hottentots and Bushmen were descended from the same original stock seems more likely' and he saw the differences between them as cultural rather than biological.

In his previously mentioned discussion of the use of 'San', Lee (1979: 30) asserted that 'The term *Bushmen* has both racist *and* sexist connotations' (Lee's emphases). In contrast, Marshall (1976: xxi) observed: 'While I believe that the name Bushman was definitely derogatory when it was first applied by European voyagers and settlers in South Africa, I have felt that it need not continue to be derogatory unless the speaker is imputing derogation in using it. In my feelings, I accord "Bushman" the dignity of any dignified race name.'

The objections to the use of 'Bushmen' are the same as those that apply to the use of 'Hottentot' (see above), and in both cases it seems clear that the names were applied to groups who were not biologically and/or culturally distinct.

KHOISAN

The term *Koisan* was coined by Schultze (1928: 211) and introduced into the English-language literature as 'Khoisan' by Schapera (1930: 5). Schultze carried out a biometric study of 'Hottentot' and 'Bushman' samples, from which he concluded that, while there was sufficient to distinguish these people from all the other races of mankind, he was unable to find differences between the two groups that were adequate to justify their being kept separate. For various reasons (see Wilson in press) Schultze's study is not acceptable today, but the name he coined has gained currency as a sort of 'blanket generic' for the peoples discussed in this paper.

Westphal (1963: 243) asserted that 'The term "Khoisan" is of no linguistic usefulness whatever.' Elsewhere (Westphal 1971: 368-369) he stated that 'Today the majority of linguists who have actually been working on these languages do not accept this classification' of the non-Bantu languages of southern Africa as belonging to the 'Khoisan family' of languages. He also commented that "'Khoisan" . . . means "the food-gathering people" viz. *Khoi*-*"person"*, *sā* *"gather food"*, *-n* *"plur. common suffix"*'. This is orthographically incorrect: the order of the first two parts would be reversed in the formation of a word with the meaning Westphal attributes to 'Khoisan', as, for example, in 'Soaqua', 'Sonqua',

'Saan' or 'Sana', the *-n(a)* suffix having the same force and meaning as *-qua* ('people') as, for example in 'Namaqua', 'Naman(a)'.

More recently, Westphal (1986 *in litt.*) has commented: '(1) The word *Khoisan* = Khoesan has no linguistic merit. It has not been shown that the Khoisan *people* spoke a uniform language nor that their languages derive from a single common ancestor. (2) The terms for the *languages* are derived from the word for "people" . . . as in the case of the word BANTU. Thus KHOE, ZHU (or whatever orthographic compromise is used), TA'A, !WI are all roots meaning "people" and could be linguistically useful. In the case of the ZHU language the language name !Xû could be used for they say: Mi okx'oi !xû = I speak !Xû.' (Westphal's emphases. The three dots after 'people' in (2) do not indicate an ellipsis but are in Westphal's letter.)

Contrary to Westphal's first point, Hiernaux (1974: 98) stated that 'There is no basis for linguistic distinction between the two groups [Hottentots and Bushmen]: the language of the Hottentots is just one of the central South African languages, close to that spoken by the Naron Bushmen.' It could, however, be argued that the Naron (= Nharo) may be the descendants of Khoikhoi-speaking herders who lost their stock and were obliged to subsist by hunting and gathering. An alternative possibility is that they may have been clients of the Nama and, like the Dama, adopted (and adapted) the Nama language.

Although Westphal is correct in stating that it has not been shown that the people spoke a common language nor that their languages derive from a single common ancestor, it has equally not been shown that they did *not*. The 'Khoisan' languages are more like each other than they are like any of the other languages of Africa, possibly even including the 'click'-using languages of the Hadza and Sandawe of East Africa. This suggests that they *are* descended from a common ancestor, or that they are amalgams of a common ancestral language with a number of other languages. Scientific linguistic studies of the 'Khoisan' languages do not extend back more than about a century and it must be borne in mind that languages do evolve, converging or diverging according to the degree of contact or isolation of their speakers. The distinctiveness of the 'Khoisan' languages from the other African languages should therefore entitle them to be included in a 'Khoisan family' of languages.

Westphal's second point is well made, but refers only to individual languages: what is needed is a corporate term to include *all* the languages, as with the peoples themselves—hence 'Khoisan'.

HERDERS AND HUNTERS

These terms, popularized by Wilson (1969: 41–74) as alternatives to the disreputable 'Hottentots' and 'Bushmen', at first glance appear to be nice, succinct terms, useful for archaeologists, who have no linguistic or, as yet, cultural or physical anthropological evidence on which to base any ascription of difference of race or culture to the people whose remains they study. However, as

Wilson was well aware and Marks (1972), Elphick (1977, 1985) and Schrire (1980) have more recently demonstrated (or reiterated), this neat dichotomy is specious.

As is abundantly clear from the early records, for the herders, by whatever names they were called, hunting, gathering, collecting, and in some cases fishing and even scavenging were an integral part of their socio-economic existence. It is thus improper to exclude, even by inference, these essential elements of the herder way of life, by calling the non-pastoralist peoples 'hunters' or any version of this name that is expanded to include one or more of the aspects mentioned above. The processes by which pastoralists lost, and sometimes regained, their stock and non-pastoralists acquired domestic animals for other than immediate consumption are discussed by the above-named authors and need not be reiterated here.

Although anthropologists engaged in southern African prehistoric and protohistoric research are aware that the herder:hunter dichotomy is not as absolute as the terms might imply, those outside the field may not be. Terms like 'herder', 'pastoralist', 'hunter-gatherer' are part of anthropology's jargon and thus need to be explained for the benefit of those not familiar with the discipline's terminology. There seems, otherwise, no good reason for replacing them with terms that, while they might be more accurate, might also be more cumbersome or even more confusing.

DISCUSSION AND CONCLUSIONS

The principal question to be answered is: what name or names can archaeologists use for the people whose remains—physical and cultural—they study from the sites they excavate? A corollary to this is that, since archaeology of necessity involves itself in other branches of anthropology (history, ethnology, physical and social anthropology, for example) in its attempts to elucidate its data, is there a terminology that can be adopted that will be acceptable to anthropology as a whole? The consensus reached at the 1971 conference, mentioned in the introduction to this paper, suggests that there is not. It is not clear, however, whether this decision was based on a genuine need to have three distinct sets of terms or was merely the result of a reluctance on the part of some of the participants to replace their particular preferences with those of others, or to identify themselves too closely with the other branches of the discipline. There seems no good reason why, for example, physical anthropologists and linguists cannot use the same names or terms, as long as it is made clear that there is no necessary correlation between physical type and language—or, for that matter, any aspect of culture. Haacke (1985 *in litt.*) has, however, mentioned that the Nama-Damara language is referred to in scientific circles as *Khoekhoegowab*. When it is necessary to refer to speakers of other 'Hottentot' dialects, for example the Hai//om, Haacke calls them 'Khoekhoe-speakers'.

Elphick (1977: xxi–xxii, 1985: xxi–xxii) considered 'a Khoikhoi to be *any person accepted as a full* (i.e. not a subordinate) *member of a Khoikhoi*

community. A Khoikhoi community was *one where a dialect of the Khoikhoi language was spoken and where pastoralism was the preferred mode of economic life* (Elphick's emphases). These three criteria, though fundamental, are minimal. Probably justifiably, Elphick avoided ascription of a physical type (see Elphick 1977: 8–10, 1985: 8–10 for his views) but there are many other cultural factors besides language and 'preferred mode of economic life' that are important, though perhaps not to a historian. By changing the name and substituting 'hunting' for 'pastoralism', Elphick's criteria could be used to define the archetypal San. Archetypes are, however, generally useful only for the definition of the opposite poles of a range, and in the human situation these rarely exist.

Elphick's criteria are not useful for archaeologists who, in the specifically Khoisan context, would probably not be able to identify the social status of the individuals whose skeletal remains might be excavated. Of language there would, of course, be no trace, and the 'preferred mode of economic life' could only be inferred. An example of the need for caution in interpreting archaeological data is that of Kaabi's kraal, visited in 1812 by Burchell (1967b: 197, pl. 4). Kaabi and his people were called Bushmen, probably on information from Burchell's Hottentot servants and guides. The illustration of the kraal shows it in many respects to be typical of a Hottentot kraal: hemispherical mat-and-wattle huts distributed in a rough circle around an open area (the kraal); and the text indicates that the people had fifty oxen and about two hundred sheep. They also had clay pots (Burchell 1967b: 45–47). That the stock were probably stolen is irrelevant: according to Elphick (1977: 11–12, 1985: 11–12) that is possibly how the 'proto-Khoi' acquired their first stock 'and became by that act the first Khoikhoi'. An archaeologist who excavated the site of Kaabi's kraal might correctly deduce it to be a pastoralist camp-site, but would be incorrect in inferring from this that it was a Khoikhoi site.

Another example of the problem of successfully applying Elphick's three criteria is the case of the Bitterbos clan of the Korana (Engelbrecht 1936: 17). On their own information, they were originally Bushmen and some of them later married into the Kats clan. These were considered to be hybrids by the others, who saw themselves still as 'pure' Bushmen. The Korana are classified as Hottentots and there is no evidence that the Bitterbosse, 'pure' or 'hybrid', were not accepted as full members of the Korana community and therefore as Hottentots, even though the 'pure' segment considered themselves Bushmen.

Elphick (1977: xxi–xxii, 1985: xxi–xxii), for reasons given, eschewed use of the name 'San', preferring instead to use terms such as 'hunters' or 'aborigines'. This places him in the somewhat invidious position of having a proper name, Khoikhoi, for one group, and common names for the others. This is analogous to referring on the one hand to 'Americans' and on the other to 'bankers' or 'natives'. The fact that hunting was an integral part of the herder and thus Khoikhoi way of life has already been mentioned, and there is no proof that the Khoikhoi were not aborigines: it has yet to be demonstrated that it was

pastoralists who moved into areas formerly only occupied by hunter-gatherers, or whether it was the practice of pastoralism that was adopted by various groups and thus moved into the areas in which it was observed from the fifteenth century onward.

Elphick (1977: 11, 1985: 11), following Westphal (1963: 259), postulated an area of origin in north-eastern Botswana for the 'proto-Khoi'. If this was indeed the case, it follows that these people differed biologically and (possibly) linguistically very little, if at all, from the other hunter-gatherer bands in the area. Assuming that it was pastoralists and not just pastoralism that moved, unless the 'proto-Khoi' bands were sufficiently large to provide an adequate number of spouses, those moving into a region would have had to acquire spouses (probably wives) from among the hunter-gatherer groups of the new region. The consequence of this would be increasing genetic and possibly linguistic diversity. The Khoikhoi pastoralists probably came in the course of time to regard themselves as superior to their non-pastoralist neighbours and would thus have chosen their marriage partners from other pastoralist communities. This would have had the effect of tending to isolate the Khoikhoi from the non-pastoralists and to increase biological, social, cultural, and linguistic similarity within their communities while increasing the differences between them and non-Khoikhoi communities. It seems likely, therefore, that any biological and linguistic distinctions that can now be observed must result from a long and complex process of interaction and/or isolation. It should consequently be anticipated that archaeological sites will cover every part of the spectrum that ranges between the archetypal pastoralist kraal and the archetypal hunter-gatherer camp, although it can be argued that the archetypal herder site does not exist, pastoralism being an addition to, rather than a replacement of, the hunter-gatherer way of life.

Parkington (1984) has suggested that there is archaeological evidence for changes in the life-style of the hunter-gatherer populations of the Cape west-coast region subsequent to the arrival of the pastoralists in that area, and again in the early historical period, when the pastoralists lost their stock to, and were displaced by, the white settlers. He has used the terms 'soaqua' and 'bushman' to denote these altered life-styles, which he considers should be differentiated from that of the aboriginal hunter-gatherers in their pristine habitat. It is felt, however, that the adoption of these terms will result in confusion, especially when they appear in papers that also use 'Soaqua', or one of its variant spellings, and/or 'Bushman'.

In conclusion, while it seems that there is no real justification for the retention of three separate sets of terms as advocated at the 1971 conference, it is considered that archaeologists, *qua* archaeologists, should confine themselves to using (socio-)economic terms such as 'herder' or 'pastoralist' and 'hunter-gatherer' when dealing with material from prehistoric sites. It is considered that the term 'forager', now gaining currency as a substitute for 'hunter-gatherer', (e.g. Lee 1979) should be abandoned. *The Concise Oxford Dictionary* (1978: 410) gives the following meanings for 'forage': 'food for horses and cattle, esp. for

horses in army; . . . collect forage from, ravage; supply with forage, get by foraging . . . search for forage; search *for* (thing), rummage'. The word is therefore better applied to the herders than to the hunters; and the implication of 'rummage' does less than justice to peoples whose modern descendants are well known to have an acute knowledge of the availability and location of the resources of their environment. When it is necessary to deal with the period from 1488 to the present, whether on the basis of sites or documentary records, the choice of terms such as 'Hottentot' or 'Khoikhoi' or 'Bushman' or 'San' should be dictated by the context or individual preference. Where necessary, the usage should be explained and justified.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

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Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text

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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

M. L. WILSON

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FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74** (33): 627–634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2** (17): 309–320.

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THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

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A RE-EVALUATION
OF THE SOUTH AFRICAN SPECIES OF
LEMBOIDES STEBBING AND *LEMBOS* BATE
(AMPHIPODA, AORIDAE)
DESCRIBED BY K. H. BARNARD (1916)

By
A. A. MYERS
&
J. LYONS

Cape Town Kaapstad

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A RE-EVALUATION OF THE SOUTH AFRICAN SPECIES OF
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 (AMPHIPODA, AORIDAE) DESCRIBED BY
 K. H. BARNARD (1916)

By

A. A. MYERS & J. LYONS

Department of Zoology, University College, Cork, Ireland

(With 9 figures)

[MS accepted 30 June 1986]

ABSTRACT

Barnard (1916) described three new species of aorid amphipod, *Lembos hypacanthus*, *Lemboides acanthiger* and *Lemboides crenatipalma* from South Africa. These were poorly figured, and have not since been fully figured or redescribed, although their distribution in South African waters has been assessed by Griffiths (1974a, 1974b, 1974c, 1975). Until now, none was known from outside South Africa.

In the present work, all three species are described and figured, *Lemboides crenatipalma* is transferred to the genus *Aorchoides* Ledoyer (family Isaicidae) and *Lembos hypacanthus* is recorded for the first time from North America. *Lemboides afer* Stebbing, a South African endemic, and the type-species of the genus, is also described and figured for comparison with *L. acanthiger*.

CONTENTS

	PAGE
Introduction.....	267
Systematics	268
<i>Aorchoides crenatipalma</i>	268
<i>Lemboides acanthiger</i>	272
<i>Lemboides afer</i>	275
<i>Lembos hypacanthus</i>	278
Discussion	281
Acknowledgements	281
References	281

INTRODUCTION

The genus *Lemboides* was described by Stebbing (1895) to include the single South African species *L. afer* Stebbing. Later, K. H. Barnard (1916) described two further South African species, *L. acanthiger* and *L. crenatipalma*, which he ascribed to the same genus. To date, no further South African species have been added to the genus. The genus has been recorded from outside South Africa (Australia and Madagascar), but the relationships of these species are not considered here (see Myers in press).

In the present work, material of all three South African species of *Lemboides*

was examined, together with material of the poorly known aorid *Lembos hypacanthus* Barnard. Preliminary investigation revealed that *Lemboides crenatipalma* should be removed from the family Aoridae and transferred to the Isaoidae. It is described and figured herein and placed in the genus *Aorchoides* Ledoyer. *Lemboides acanthiger* is difficult to assign and brings into question the validity of the genus *Lemboides*. Stebbing (1895) gives only a single character separating *Lemboides* from *Lembos*, viz.: male gnathopod 1 'fifth joint is much broader and longer than sixth'. Whilst this is true of *Lemboides afer*, the type-species, it does not apply to *L. acanthiger*, in which the carpus and propodus of the male gnathopod 1 are subequal, just as they are in *Lembos hypacanthus*. However, synonymization of *Lemboides* with *Lembos* would not be advisable at this stage, since *Lemboides* differs from the type-species of *Lembos*, i.e. *L. websteri* (though not from most other species of the genus), by the short peduncle of uropod 3. The splitting of the genus *Lembos* into several component genera is being proposed elsewhere (Myers in press). A character of phylogenetic significance is exhibited by the maxilliped of *L. hypacanthus*. Wing-like extensions occur on the anterior margin of the inner and outer plate of this appendage. This character is also present in some, but not all, *Microdeutopus* species, and in *L. websteri*. *Lembos websteri* is unique among *Lembos* in having the uropod 3 rami subequal and equal in length with the elongate peduncle, a character shared with *Microdeutopus* sensu stricto. Thus *L. websteri* in its maxilliped and uropod 3 structure aligns itself with *Microdeutopus* rather than with other *Lembos* species. This is nomenclaturally confusing, since *L. websteri* is the type-species of the genus. *Lembos hypacanthus*, which forms a geminate pair with *L. websteri*, is here shown to be transatlantic. In the East Atlantic *L. websteri* and *L. hypacanthus* are widely allopatric. In the West Atlantic their distributions have not yet been worked out, but they are probably closely allopatric or parapatric.

SYSTEMATIC SECTION

Family Isaoidae Dana, 1853

Genus *Aorchoides* Ledoyer, 1972

Aorchoides crenatipalma (K. H. Barnard, 1916) comb. nov.

Figs 1A, 2-3

Lemboides crenatipalma K. H. Barnard, 1916: 240, pl. 28 (figs 9-10). Griffiths, 1976: 34, fig. 18C.

Type locality

Baboon Point ENE, distant 13 miles (off Saldanha Bay), 32 fathoms.

Material examined

SAM-A18949, 13 ♂, 24 ♀, Skrywershoek, Langebaan Lagoon, mud, 26 April 1949, UCT LB189P. SAM-A19396, 1 ♂, 1 ♀, 26°35'S 15°01'E, 71 m, rock, 10 June 1963, UCT SWD13T. SAM-A19397, 1 ♂, 1 ♀, 25°51'S 14°50,7'E, 60 m, 13 November 1948, UCT AFR1335A. SAM-A19398, 3 ♂, 1 ♀, 32°44'S 18°01'E, 11 m, 22 September 1960, UCT WCD68B.

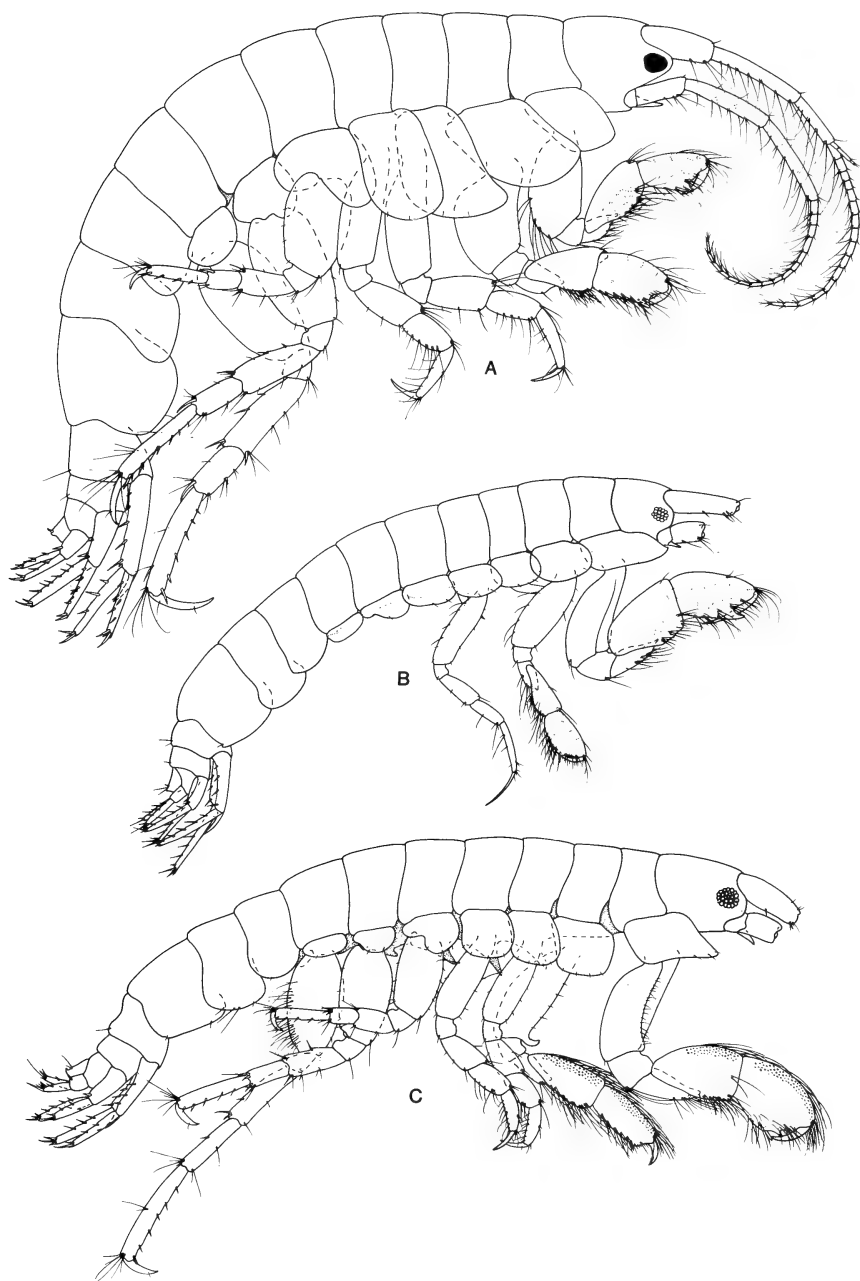


Fig. 1. A. *Aorchoides crenatipalma* (K. H. Barnard), male, 9,0 mm, Skrywershoek.
B. *Lemboides acanthiger* K. H. Barnard, male, 5,5 mm, Natal.
C. *Lembos hypacanthus* K. H. Barnard, male, 6,0 mm, Dalebrook (False Bay).

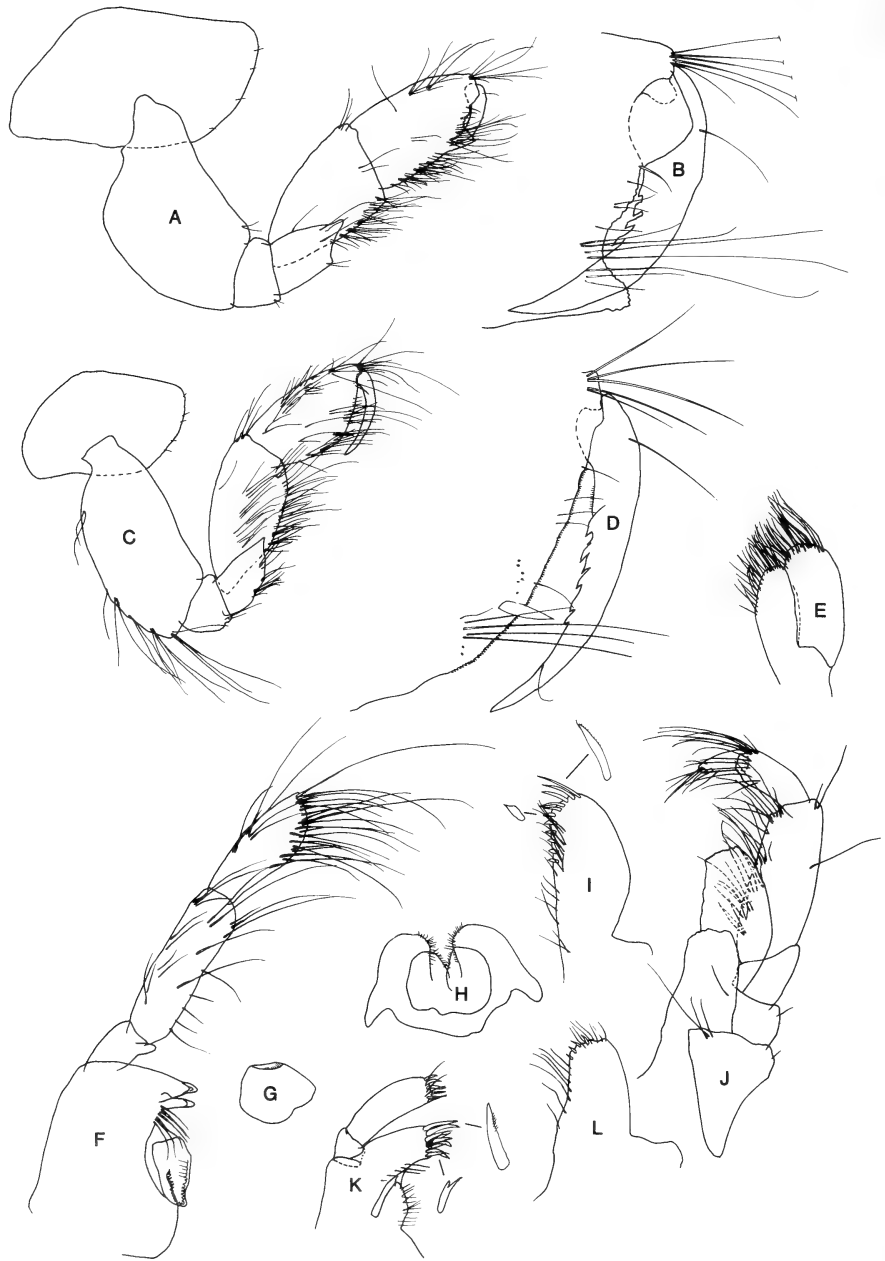


Fig. 2. *Aorchooides crenatipalma* (K. H. Barnard), male, 7.0 mm, Langebaan Lagoon. A. Gnathopod 2. B. Gnathopod 2 palm (enlarged). C. Gnathopod 1. D. Gnathopod 1 palm (enlarged). E. Maxilla 2. F. Mandible. G. Labrum. H. Labium. I, J, L. Maxilliped. K. Maxilla 1.

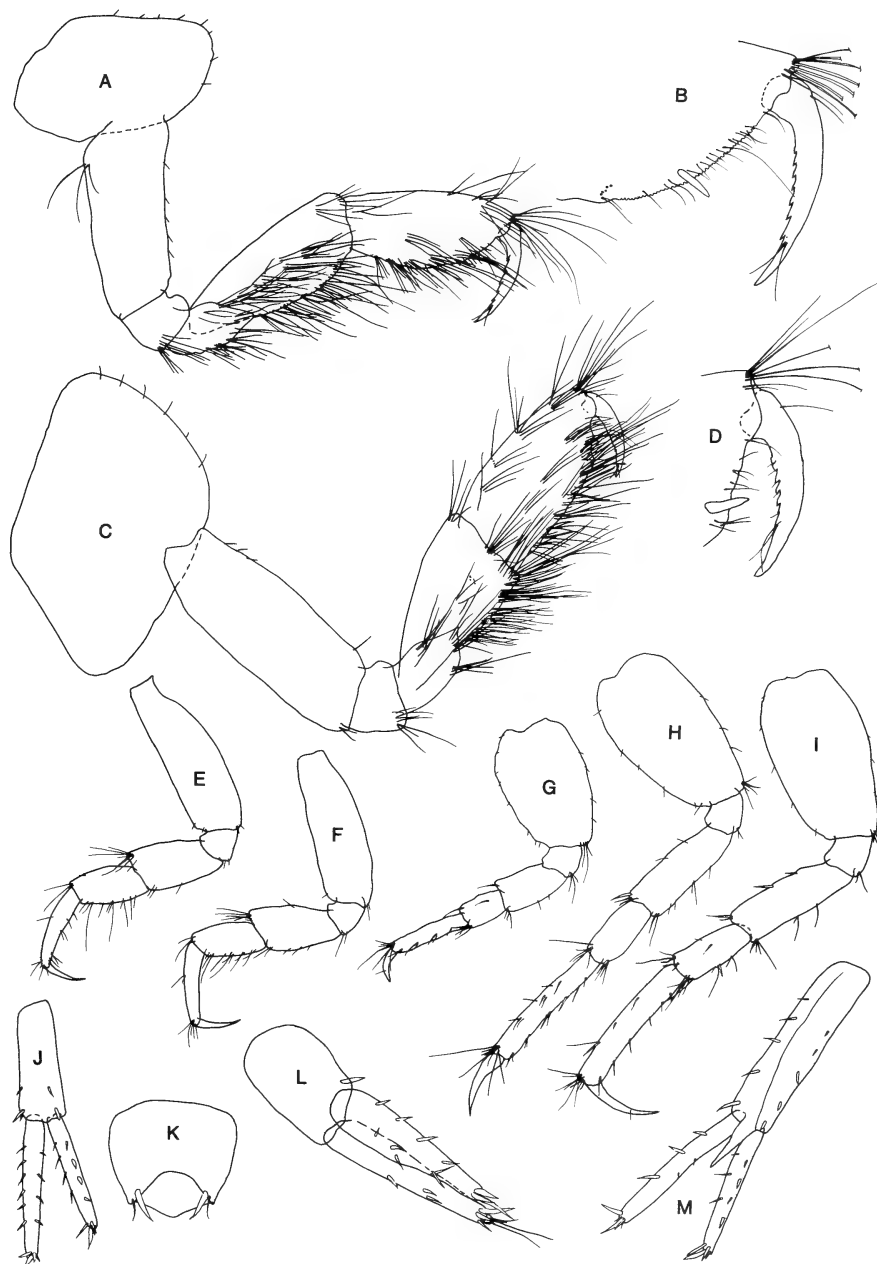


Fig. 3. *Aorchoides crenatipalma* (K. H. Barnard), female, 8.0 mm, Langebaan Lagoon. A. Gnathopod 1. B. Gnathopod 1 palm (enlarged). C. Gnathopod 2. D. Gnathopod 2 palm (enlarged). E. Pereopod 3. F. Pereopod 4. G. Pereopod 5. H. Pereopod 6. I. Pereopod 7. J. Uropod 2. K. Telson. L. Uropod 3. M. Uropod 1.

Description

Head with eye lobes strongly produced, subocular margin strongly excavate, eye situated in ocular lobe. Antennae 1 and 2 subequal, setose, accessory flagellum 3-articulate, antenna 2 slender. Labium mandibular lobes only moderately produced, subacute. Mandibular palp article 2 longer than article 3, article 3 truncate, approximately parallel-sided. Coxae 1–4 longer than broad, coxa 3 longest, produced forward distally. Gnathopod 1 ♂ basis enlarged, posterior distal margin with long setae, carpus slender, longer than propodus, propodus slender, palm evenly rounded (subadults) or produced into weak triangular defining tooth (hyperadults). Gnathopod 1 ♀ slender, carpus longer than propodus. Gnathopod 2 ♂ robust, basis maximally two-thirds as broad as long, carpus longer than propodus, palm defined by triangular tooth. Gnathopod 2 ♀ slender, propodus a little longer than carpus, palm irregular. Pereopod 7 scarcely longer than pereopod 6. Epimera 1–3 rounded. Uropod 1 peduncle longer than rami with interramal tooth. Uropod 2 inner ramus longer than outer and longer than peduncle, which lacks an interramal tooth. Uropod 3 peduncle short, inner ramus one and a half times length of peduncle. Telsonic crests each with a stout spine.

Remarks

This species shows numerous characters that indicate its isaeid ancestry. Notably, the setose subequal antennae, slender antenna 2, extended eye lobes, strongly regressed subocular margin. The deep coxae and short pereopod 7 immediately distinguish it from *Lembos* and *Lemboides* species.

Distribution

Southern African endemic.

Family **Aoridae** Stebbing, 1899

Genus *Lemboides* Stebbing, 1895

Lemboides acanthiger K. H. Barnard, 1916

Figs 1B, 4–5

Lemboides acanthiger K. H. Barnard, 1916: 239, pl. 28 (figs 7–8). Griffiths, 1976: 34, fig. 18A.

Type locality

Umvoti River mouth N by W $\frac{1}{4}$ W, distant 15 miles (Natal), 56 fathoms.

Material examined

SAM-A18947, 2 ♂, 1 ♀, Natal, 29°53'S 31°06'E, 71 m, mud, 13 July 1959, UCT NAD27C.

Description

Head with eye lobes moderately produced, eye small. Antennae missing in all material examined. Labium mandibular lobes acute. Mandibular palp article 3



Fig. 4. *Lembooides acanthiger* K. H. Barnard, female, 6,0 mm, Natal. A. Gnathopod 2 palm (enlarged). B. Gnathopod 2. C. Labrum. D. Labium. E. Gnathopod 1. F. Gnathopod 1 palm (enlarged). G. Mandible. H. Mandible palp article 3 (enlarged). I. Maxilla 1. J, M, N. Maxilliped. K. Mandible—spine row and lacinia mobilis (enlarged). L. Maxilla 2.

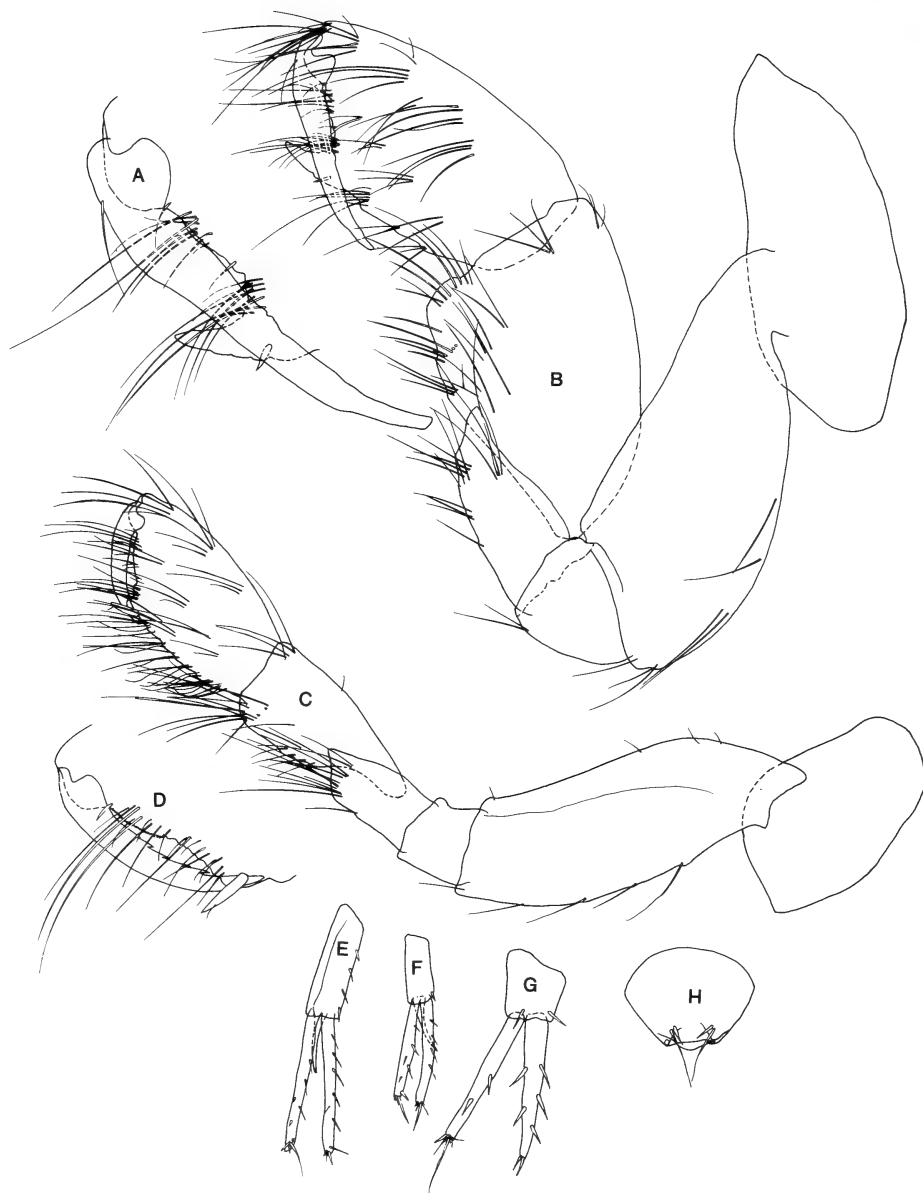


Fig. 5. *Lembooides acanthiger* K. H. Barnard, male, 6.0 mm, Natal. A. Gnathopod 1 palm (enlarged). B. Gnathopod 1. C. Gnathopod 2. D. Gnathopod 2 palm (enlarged). E. Uropod 1. F. Uropod 2. G. Uropod 3. H. Telson.

longest, terminally falcate. Coxae 1–4 shallow, coxa 1 elongate, broader than deep, produced forward, subacute. Gnathopod 1 ♂ basis robust, carpus and propodus subequal in length, propodus palm irregular, defined by strong acute tooth, dactylus very strongly overlapping palm. Gnathopod 1 ♀ slender, propodus a little longer than carpus, palm weakly sinuous and crenulate, dactylus elongate, overlapping palm. Gnathopod 2 ♂ carpus and propodus subequal in length but propodus broader, palm weakly concave, crenulate, dactylus overlapping palm. Gnathopod 2 ♀ similar to that of ♂ but basis more slender, palm regular. Pereopods 5–7 missing in all material examined. Epimera 1–2 rounded, epimeron 3 with small posterodistal tooth. Uropods 1–2 with strong interramal tooth. Uropod 1 peduncle a little shorter than subequal rami. Uropod 2 peduncle very short, rami more than twice length of peduncle, telsonic crests each with a pair of setae.

Remarks

Lemboides acanthiger and *L. afer* together resemble Atlanto–East Pacific *Microdeutopus* (raised to generic level in Myers in press) in the very short peduncle and spinose rami of uropod 3. By contrast, East Atlantic–Mediterranean *Microdeutopus* have elongate uropod 3 peduncles, whilst Indo-Pacific *Lembos* sensu lato have elongate setae on the rami. For the present, the genus *Lemboides* is retained for these two species.

Distribution

Southern African endemic.

Lemboides afer Stebbing, 1895

Figs 6–7

Lemboides afer Stebbing, 1895: 209, pls 9–10. K. H. Barnard, 1932: 222, fig. 137. Griffiths, 1976: 34, fig. 18B.

Type locality

Cape of Good Hope.

Material examined

SAM–A19399, 3 ♂, 2 ♀, off Oatland Point, 34°12'S 18°29'E, 33–36 m, 5 March 1952, UCT FAL31H. SAM–A19400, 1 ♂, 1 ♀, 34°19.3'S 18°32.3'E, 58 m, 8 September 1956, UCT TRA111P. SAM–A18948, 20 ♂, 26 ♀, Skrywershoek, Langebaan Lagoon, LWS and below, 26 April 1949, UCT LB191S.

Description

Head with eye lobes moderately produced, eye small. Antennae weakly setiferous; antenna 1 short, about one-third body length, antenna 2 subpediform, shorter than antenna 1. Labium mandibular lobes acute. Mandibular palp



Fig. 6. *Lembooides afer* Stebbing, female, 7.0 mm, Oatland Point. A. Gnathopod 2. B. Labrum. C. Maxilla 2. D. Maxilla 1. E. Labium. F. Gnathopod 2 palm (enlarged). G. Gnathopod 1. H. Gnathopod 1 palm (enlarged). I. Mandible. J. Mandible palp article 3 (enlarged). K. Mandible—spine row and lacinia mobilis (enlarged). L-N. Maxilliped.

articles 2 and 3 subequal in length, article 3 with distal part of anterior margin weakly concave. Coxae 1–4 shallow; coxa 1 elongate, broader than deep, rounded. Gnathopod 1 ♂ basis robust, carpus enormous with posterodistal margin weakly produced into irregular lobe, propodus short, a little over one-half length of carpus, palm defined by two irregularly triangular processes, dactylus short. Gnathopod 1 ♀ carpus only a little longer than propodus, propodus with crenulated palm. Gnathopod 2 ♂ basis with anterior margin produced into a crenulated flange, carpus enlarged, anterior margin with long setae, propodus short, a little over one-half length of carpus, palm with V-shaped crenulate-sided excavation defined by a triangular tooth bearing a spine, dactylus short. Gnathopod 2 ♀ basis elongate, anterior margin with long setae, basis swollen medially, anterior margin with very long sieve-setae, propodus elongate and slender, a little longer than carpus, palm short, irregular, defined by two spines, dactylus short, fitting palm. Pereopod 7 distinctly longer than pereopod 6. Epimera 1–3 rounded. Uropods 1–2 with interrampal peduncular tooth. Uropod 1 peduncle and rami subequal. Uropod 2 inner ramus longer than outer

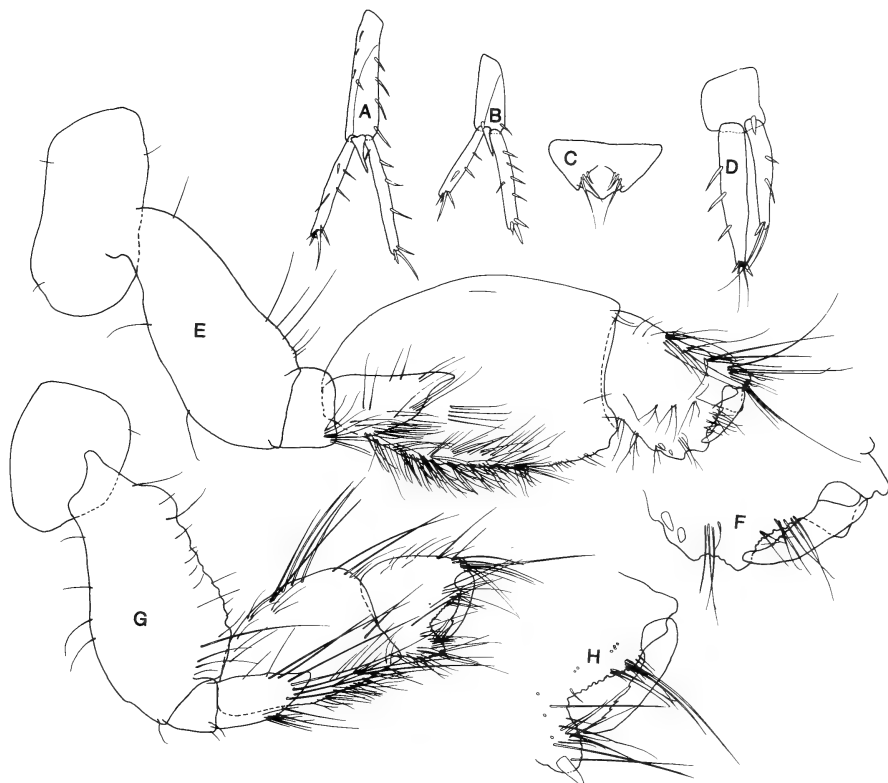


Fig. 7. *Lembooides afer* Stebbing, male, 6.0 mm, Oatland Point. A. Uropod 1. B. Uropod 2. C. Telson. D. Uropod 3. E. Gnathopod 1. F. Gnathopod 1 palm (enlarged). G. Gnathopod 2. H. Gnathopod 2 palm (enlarged).

ramus and longer than peduncle. Uropod 3 peduncle very short, inner ramus longer than outer and more than twice length of peduncle. Telsonic crests each with 4–5 setae.

Remarks

For relationships, see comments under previous species.

Distribution

Southern African endemic.

Lembos hypacanthus K. H. Barnard, 1916

Figs 1C, 8–9

Lembos hypacanthus K. H. Barnard, 1916: 237, pl. 28 (figs 5–6). Griffiths, 1976: 34, fig. 18D. *Lembos* sp. Fox, 1978: 162.

Type locality

Sea Point, near Cape Town.

Material examined

SAM-A18951, 1 ♂, 1 ♀, Dalebrook (False Bay), intertidal, 14 September 1955, UCT CP439E. 67 ♂, 59 ♀, 21 immature, Brevard C, Florida. 13 ♂, 24 ♀, North Carolina.

Description

Head with eye lobes moderately produced; eye of medium size. Antennae weakly setiferous; antenna 1 about two-thirds body length, antenna 2 subpediform, shorter than antenna 1. Labium mandibular lobes acute. Mandibular palp article 3 longer than 2, distinctly falcate. Coxae 1–4 shallow; coxa 1 anterodistal margin produced, acute. Gnathopod 1 ♂ basis robust, inner face with a proximal tooth, carpus and propodus subequal in length and breadth, anterior margin densely setose, propodus with a short crenulate palm, followed by a deep excavation posterior to which is a slender tooth and a defining hump bearing a spine, dactylus short. Gnathopod 1 ♀ propodus slightly longer than carpus, palm irregularly rounded, defined by a spine. Gnathopod 2 ♂ basis with falcate anterodistal tooth, carpus and propodus elongate, especially so in American material, anterior margin of both podomeres densely setose, dactylus short but overlapping short palm. Gnathopod 2 ♀ similar to that of ♂ but a little less setose. Pereopod 7 distinctly longer than pereopod 6. Epimera 1–2 rounded. Epimeron 3 with small posterodistal tooth. Uropod 1 peduncle and inner ramus subequal, inner ramus longer than outer. Uropod 2 peduncle shorter than inner ramus, inner ramus longer than outer. Uropod 3 peduncle unexpanded, rami subequal, a little longer than peduncle. Telsonic crests each with a pair of unequal length setae.

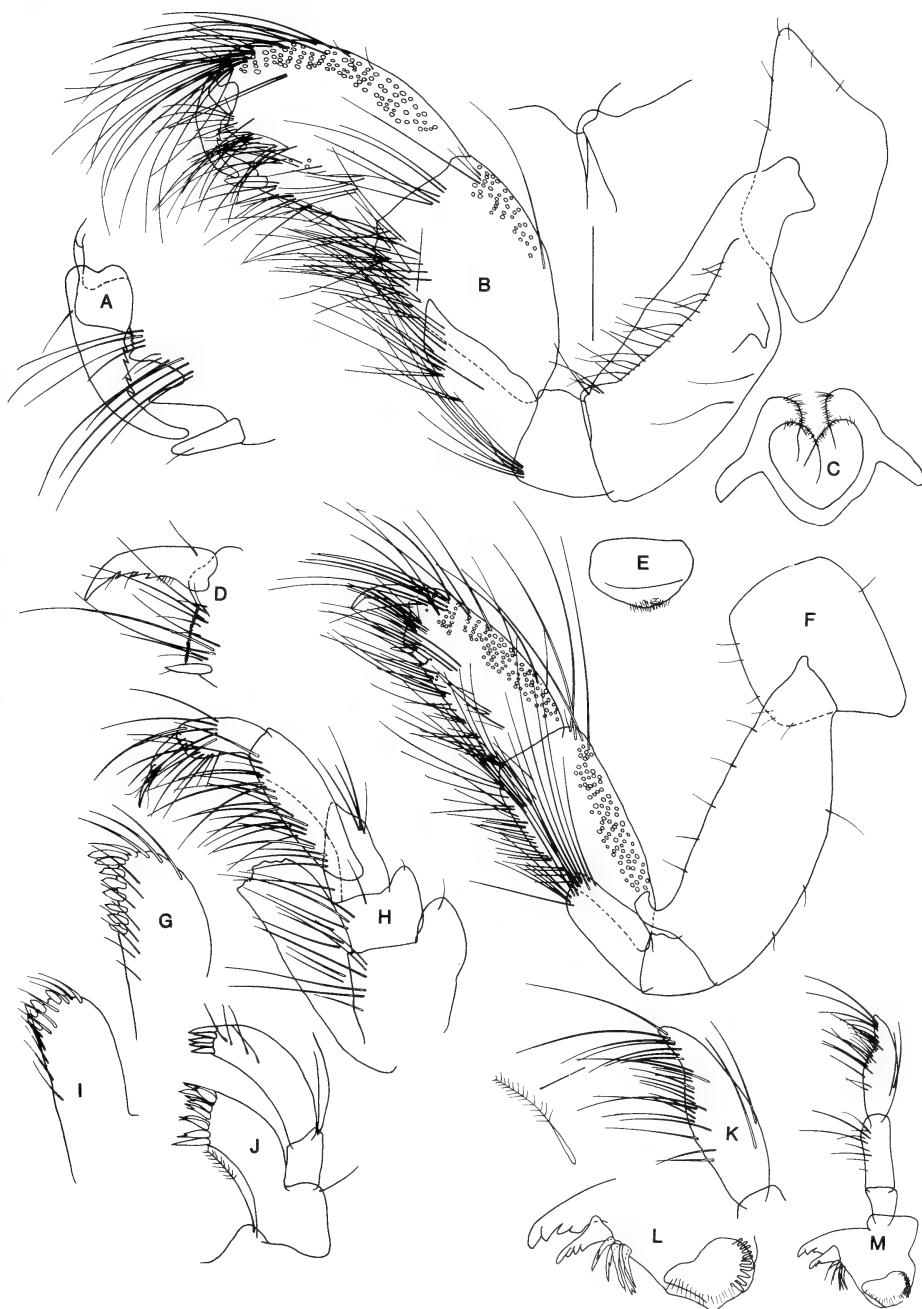


Fig. 8. *Lembos hypacanthus* K. H. Barnard, male, 6.0 mm, False Bay. A. Gnathopod 1 palm (enlarged). B. Gnathopod 1. C. Labium. D. Gnathopod 2 palm (enlarged). E. Labrum. F. Gnathopod 2. G-I. Maxilliped. J. Maxilla 1. K. Mandible palp article 3 (enlarged). L. Mandible—spine row and lacinia mobilis (enlarged). M. Mandible.

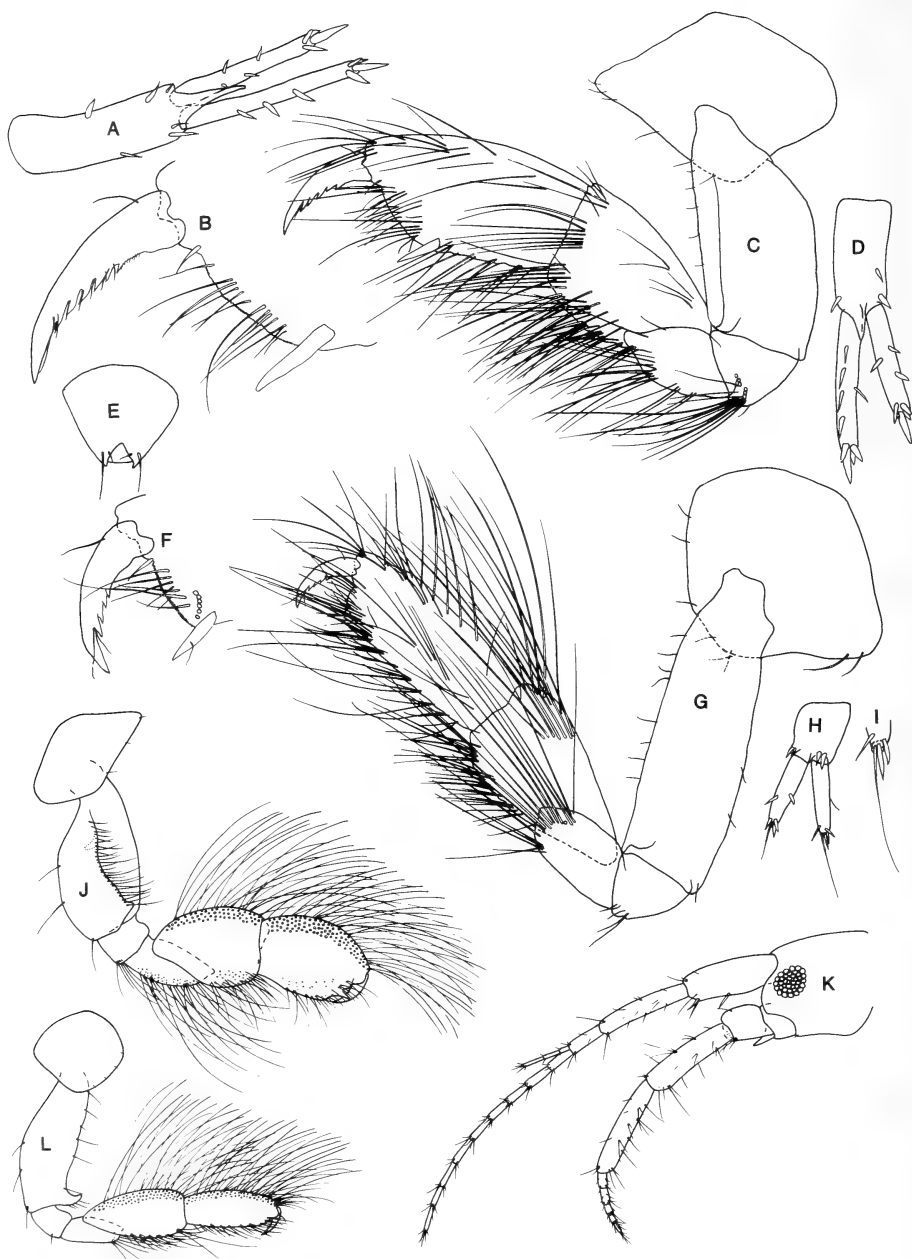


Fig. 9. *Lembos hypacanthus* K. H. Barnard. A-I. Female, 5,5 mm, False Bay. A. Uropod 1. B. Gnathopod 1 palm (enlarged). C. Gnathopod 1. D. Uropod. E. Telson. F. Gnathopod 2 palm (enlarged). G. Gnathopod 2. H. Uropod 3. I. Uropod 3—tip of inner ramus. J-L. Male, 6,0 mm, North Carolina. J. Gnathopod 1. K. Head. L. Gnathopod 2.

Remarks

The maxilliped flanges and form of the male gnathopod 1 clearly place this species close to *L. websteri*, the type-species of the genus.

Distribution

Originally thought to be a South African endemic, this species is now known to occur also in the West Atlantic.

DISCUSSION

The present study has revealed a close biogeographical relationship between the *Lemboides* and *Lembos* species of southern Africa and those of the Atlanto-East Pacific. *Lemboides* sensu stricto has its closest relationships with Atlanto-East Pacific *Microdeutopus*, and *Lembos hypacanthus* is now shown to be transatlantic. *Lembos websteri*, the sister species closest to *L. hypacanthus*, is also known from both eastern North America and the north-eastern Atlantic-Mediterranean. These distributions may be best explained as relictual, resulting from the opening-up of the Atlantic by tectonic activity in the early Tertiary. This contrasts with what is known of the distribution of the genus *Aora*, which is also present in southern Africa and appears to have Gondwanian or transantarctic affinities.

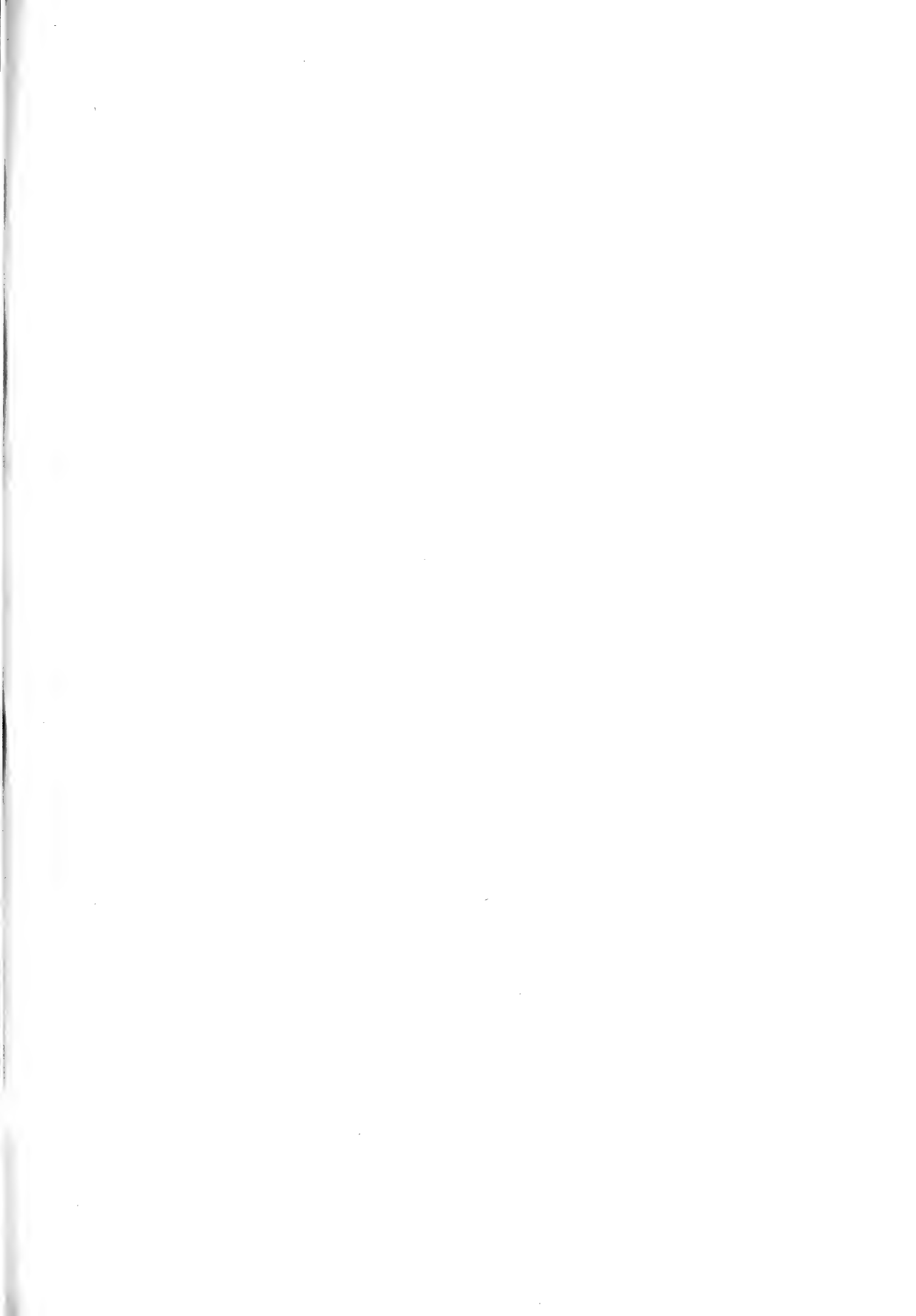
ACKNOWLEDGEMENTS

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Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

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A. A. MYERS

&

J. LYONS

A RE-EVALUATION
OF THE SOUTH AFRICAN SPECIES OF
LEMBOIDES STEBBING AND *LEMBOS* BATE
(AMPHIPODA, AORIDAE)
DESCRIBED BY K. H. BARNARD (1916)

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(continued inside back cover)

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ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

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MIOCENE SUIDAE FROM ARRISDRIFT,
SOUTH WEST AFRICA-NAMIBIA

By
MARTIN PICKFORD

Cape Town

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MIOCENE SUIDAE FROM ARRISDRIFT, SOUTH WEST AFRICA-NAMIBIA

By

MARTIN PICKFORD

Institut de Paléontologie, 75005, Paris, France

(With 3 figs and 3 tables)

[MS accepted 30 April 1987]

ABSTRACT

Two taxa of small suids occur at the early middle Miocene locality of Arrisdrift, South West Africa-Namibia. Of these, the more abundantly represented is *Lopholistriodon moruoroti*, a small listriodont previously known from equatorial sites in Kenya. The second, poorly represented species is a small pig with bunodont dentition, possibly related to the subfamily Tetraconodontinae. The relationships of the two species and their implications for biostratigraphy and palaeozoogeography are explored, and it is concluded that the Arrisdrift strata post-date the first of the Neogene Dispersal Phases of Thomas, dated about 17.5 m.y. ago, but that they are unlikely to be as young as 14 m.y. old.

CONTENTS

	PAGE
Introduction.....	283
Systematic description	284
Discussion	293
Acknowledgements	294
References	295

INTRODUCTION

Arrisdrift, a locality near the Orange River in South West Africa-Namibia, is the only known middle Miocene African fossil locality south of the Nyanza Rift Valley sites of Maboko and Nyakach, Kenya, which occur a few kilometres south of the equator (Pickford 1984). It is evidently somewhat younger, on the basis of its faunal content, than other fossiliferous strata in South West Africa-Namibia (Stromer 1926) at Langental, Elizabethfeld, Bogenfels and Fiskus (Hendey 1984). The distance between the equatorial Kenyan sites and Arrisdrift is more than 3 000 km; yet some of the fossil Suidae from the two regions appear, on the basis of available evidence, to be comparable, which suggests that the two regions were possibly biostratigraphically and ecologically similar.

Corvinus & Hendey (1978) and Hendey (1978, 1984) suggested, on the basis of the aspect of the entire mammalian fauna, that Arrisdrift may be about 16-15 m.y. old, an estimate that seems reasonable. The ruminants and hyracoids indicate an age slightly younger than Maboko and Buluk, Kenya. The latter site has been radiometrically dated to be about 17.2 m.y. (MacDougall & Watkins 1985), while the former is known to be older than 13 m.y. (Bishop *et al.* 1969).

Newly discovered strata at Nachola, northern Kenya, have yielded a comparable fauna, dated about 15,5 m.y. old (work in progress). The Arrisdrift faunas are probably older than those from Fort Ternan, Kenya, dated to be about 14 m.y. (Bishop *et al.* 1969) but possibly somewhat younger (work in progress).

There can be little doubt, therefore, that the Arrisdrift fauna is, in a broad sense, early middle Miocene in age, i.e. somewhere between 17,2 and 14 m.y. old. Its importance is very great, providing, as it does, the only glimpse of a middle Miocene terrestrial fauna for virtually the entire subequatorial expanse of Africa. The zoogeographic and biostratigraphic implications of this important site cannot be overstressed. This detailed systematic description of the suid remains from Arrisdrift will hopefully go some way towards augmenting the already valuable data and preliminary interpretations of the mammal fauna of the site.

The fossil suid material includes cranio-dental fragments of a small lophodont species, teeth and mandible fragments of an unidentified bunodont suid, and postcranial bones that, on the basis of their size, could belong to either of the two forms. The material is in the collections of the South African Museum and bears the catalogue prefix SAM-PQ, which is omitted from the accession numbers given in the text.

SYSTEMATIC DESCRIPTION

Family **Suidae** Gray, 1821

Subfamily Listriodontinae Simpson, 1945

Genus *Lopholistriodon* Pickford & Wilkinson, 1975

Type-species: Lopholistriodon kidogosana Pickford & Wilkinson, 1975.

Diagnosis

A genus that differs from other genera of the subfamily by its small size and the extreme development of the transverse crests in the molars and fourth premolars, with the suppression of accessory cusps. The upper premolars possess enlarged cingula and wide cingular platforms. The nasal ridge is narrow. (After Pickford 1986.)

Lopholistriodon moruoroti Wilkinson, 1976

Figs 1, 2A–C, 3D

Listriodon sp. Harris & Watkins, 1974: 576–577.

Lopholistriodon sp. D Pickford & Wilkinson, 1975: 133.

Lopholistriodon moruoroti Wilkinson, 1976: 242–245, pl. 9 (fig. B). Hendey, 1978: 23. Pickford, 1986: 56–58.

Diagnosis

A small species of *Lopholistriodon* in which the diastemata are rather short, P¹ immediately behind C, P² separated from P¹. Hypoconid crests better developed than in *L. kidogosana*.

Holotype

KNM-MO 5, mandible with roots of left I_{1-3} , complete C_1 , P_{3-4} , and M_{1-3} ; right I_{1-2} , root I_3 , complete C_1 , P_2-M_3 (Wilkinson 1976, pl. 9 (fig. B)), housed in the Kenya National Museum, Nairobi, Kenya.

Horizon

Early middle Miocene, possibly about 16 million years.

Type locality

Moruorot, Kenya.

Distribution

Moruorot, Buluk and Maboko, Kenya; Arrisdrift, South West Africa-Namibia.

Material

AD49: upper canine; AD135: left M_3 ; AD136: left maxilla with P^4-M^3 ; AD138+316+317: snout with left and right I^1 , left I^2 , left and right C , and roots of left P^1 and right I^3 ; AD636: left M_3 ; AD769: lower molar fragment; AD990: upper canine; AD1727: right I_2 ; AD1753: left M^2 ; AD2196: right M_3 broken, in mandible fragment; AD2411: left M^1 ; AD2535: mesial part of right dM_4 ; AD2565: left M^1 and broken M^2 ; AD2658: left dM_4 in mandible fragment; AD2692: distal portion of right M_3 ; AD2927: right M_3 and distal part of M_2 in mandible fragment; AD3014: right upper canine; AD3015: right I_2 ; AD3276: distal portion of right dM_4 .

Description

Fossil listriodont material from Arrisdrift consists of at least 21 cranio-dental fragments, which can confidently be assigned to a small lophodont pig species that was identified by Hendey (1978) as *Lopholistriodon moruoroti*. In addition there are five postcranial fragments that may belong to this species (see separate section in which the postcranial elements are described).

The Arrisdrift specimens include a snout, hitherto not represented among previously described material; the bulk of the sample duplicates existing information.

Snout. AD138 is the only known snout of this species; it can be compared with that of *Lopholistriodon kidogosana* from Ngorora, Kenya. The Arrisdrift specimen is crushed and warped (Fig. 1A-D) but details of its anatomy can be discerned reasonably satisfactorily. The nasal bones are broken anteriorly but are wide and stout. The premaxilla is slightly spatulate in palatal view, the area in front of the I^3-C diastema being wider than the width at the diastema. The roots of the central incisors are widely separated although the mesial edges of the crowns met mesially in life. The roots of I^{1-3} are close together.

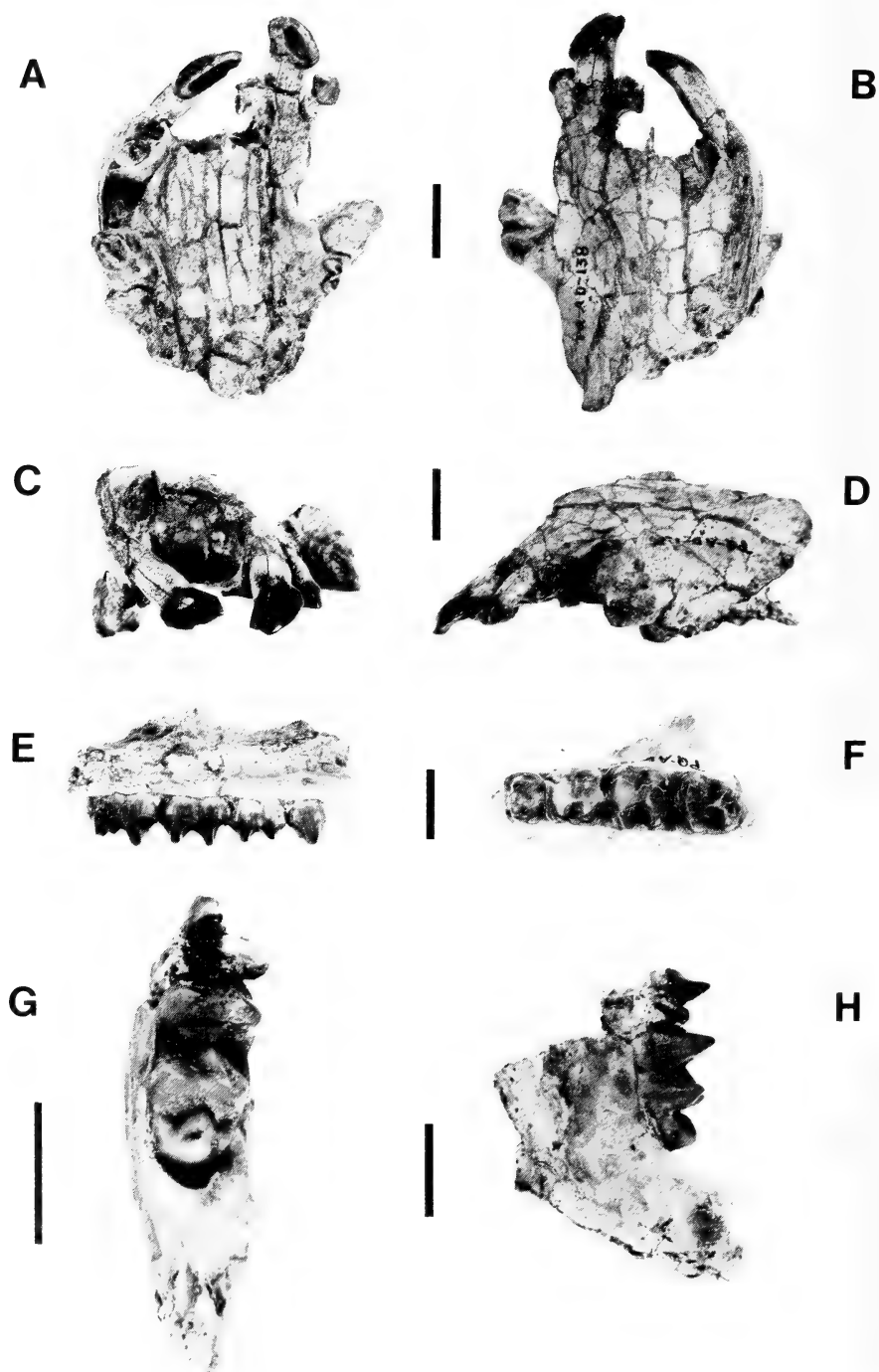


Fig. 1. *Lopholistriodon moruoroti*. A-D. SAM-PQ-AD138: snout with left and right I^1 , left I^2 , both canines, and roots of left P^1 . A. Occlusal view. B. Dorsal view. C. Anterior view. D. Left lateral view. E-F. SAM-PQ-AD136: left maxilla with P^4 - M^3 . E. Lingual view. F. Occlusal view. G-H. SAM-PQ-AD2927: right mandible fragment with part of M_2 and complete M_3 . G. Occlusal view. H. Lingual view. Scales = 1 cm.

TABLE 1
Dimensions (in mm) of the teeth of *Lopholistriodon moruoroti*.

Teeth	Specimen	Length	Breadth
<i>Upper dentition</i>			
Left I ¹	AD316	10,5	4,6
Right I ¹	AD316	12,0	4,8
Left I ²	AD317	5,5	3,6
Left \overline{C}	AD138	10,0	7,8
Right \overline{C}	AD3014	7,8	5,6
Right \overline{C}	AD138	10,3	7,2
Right \overline{C}	AD49	8,7	7,9
Left P ⁴	AD136	5,5	8,4
Left P ⁴	Mor	6,8	7,9
Left M ¹	AD136	9,5	9,1
Left M ¹	AD2411	9,9	9,3
Left M ¹	AD2565	9,8	9,1
Left M ¹	Mor	9+	8,8
Left M ²	AD2565	—	11,0
Left M ²	AD136	10,7	10,5
Left M ²	AD1753	10,9	10,2
Left M ²	Mor	10,5	10,4
Left M ³	AD136	11,3	10,0
Left M ³	Mor	11,0	10,2
<i>Lower dentition</i>			
Right I ₂	AD1727	4,3	3,2
Right I ₂	AD3015	—	4,2
Left M ₃	AD636	12,5+	8,1
Left M ₃	AD135	14,0	8,8
Right M ₃	AD2927	15,0	8,2
Right M ₃	AD2196	14,0	—
Right M ₃	Mor	14,5	8,0
Left dM ₄	AD2658	12,1	5,1
Right dM ₄	AD3276	—	4,0

The premaxillary diastema that housed the lower canine during occlusion has a sharp-edged dorsal ridge, which reaches upwards and laterally above the upper canine to form a supracanine flange, as in *L. kidogosana*.

The upper canines point antero-laterally and slightly downwards, suggesting the possibility that this individual was a female. The palate between the two canines is rather broken but seems originally to have been quite flat. The P¹ roots are close to the upper canine and there is a substantial ridge forming the alveolar process for P¹. Apart from size, the only major difference from *L. kidogosana* is the presence of P¹ roots close to the upper canines.

The upper dentition. I¹ is well preserved in the snout (AD138). It is mesiodistally elongated with a large lingual cingulum; a lingual fossette above the cingulum is wide and quite deep. The occlusal edge is worn, exposing dentine,

and the pattern of dentine exposure and the wavy labial surface of the enamel suggest that this tooth, when unworn, had terminal pectinations as in *Lopholistriodon kidogosana* and *Listriodon splendens*.

I¹ roots are long and housed in prominent juga, which form the lower lateral parts of the nasal aperture. The roots of I²⁻³, in contrast, are very small. I² is a very small tooth, with a lingual cingulum, a triangular crown in lingual view, with its main wear facet anteriorly situated. The incisive foramina are large and situated in line with the I² roots, far forward in the palate.

The canines are closed-rooted, tusk-like teeth tapering from the cervix both crownwards and rootwards. A single large anterior facet is worn by occlusion with the lower canine (Fig. 3D). This facet is almost vertically oriented, and its palato-dorsal dimension is greater than its mesiodistal width.

Maxilla and posterior upper dentition. AD136 is a left maxilla with P⁴-M³ and part of the zygomatic process of the maxilla (Fig. 1E-F). The distal surface of the zygomatic root is opposite M³ and there is a small projection of maxilla behind M³. The greater palatine foramen is close to the edge of the palate on a level with the front of M².

P⁴ is a markedly lophodont tooth, surrounded anteriorly, buccally and distally by a cingulum. The disto-buccal cusp is greatly reduced, appearing as a slight cusplet on the disto-buccal crest. The molars are all strongly bilophodont, but there are ridges leading into the median valley from both lophs, forming characteristic low antero-posterior crests in the midline of the teeth. All the upper molars bear peripheral cingula.

Mandibles and lower dentition. AD2658 is a juvenile mandible with left dM₄ and part of the symphysis up to the midline (Fig. 2A-B), which indicates that this species had a spatulate symphysis as in the genus *Listriodon*. The dM₄ is comprised of three lophs, the distal loph being the widest. Antero-posterior crests run into the median and distal transverse valleys of the tooth.

AD2927 (Fig. 1G-H) and 2196 are small mandibular fragments each containing M₃. The mandibles are gracile, the roots of M₃ are fused buccolingually, and the ascending ramus is well behind M₃ as in *Listriodon* species, in contrast to most other suids, where it hides the rear of M₃ in lateral view.

The lower third molars are comprised of two main lophs, behind which is a well-developed, centrally positioned talonid. The anterior lophs are extremely lophodont, with most of the grooves and crests suppressed, but the median accessory cusp is joined by a well-developed crest to the hypoconid. In the latter respect, this tooth differs from that of *L. kidogosana*, in which the homologous crest is almost completely suppressed. The median valley is deep and U-shaped, and is divided into two portions separated by the median accessory cusp. The talonid is comprised of a single centrally positioned cusp, which is probably an enlarged hypoconulid. On either side of it, mesially and laterally, it has low cingula.

In M₂, which is poorly represented in the Arrisdrift collection (Fig. 1H), the hypoconulid is small and positioned close behind the distal loph.

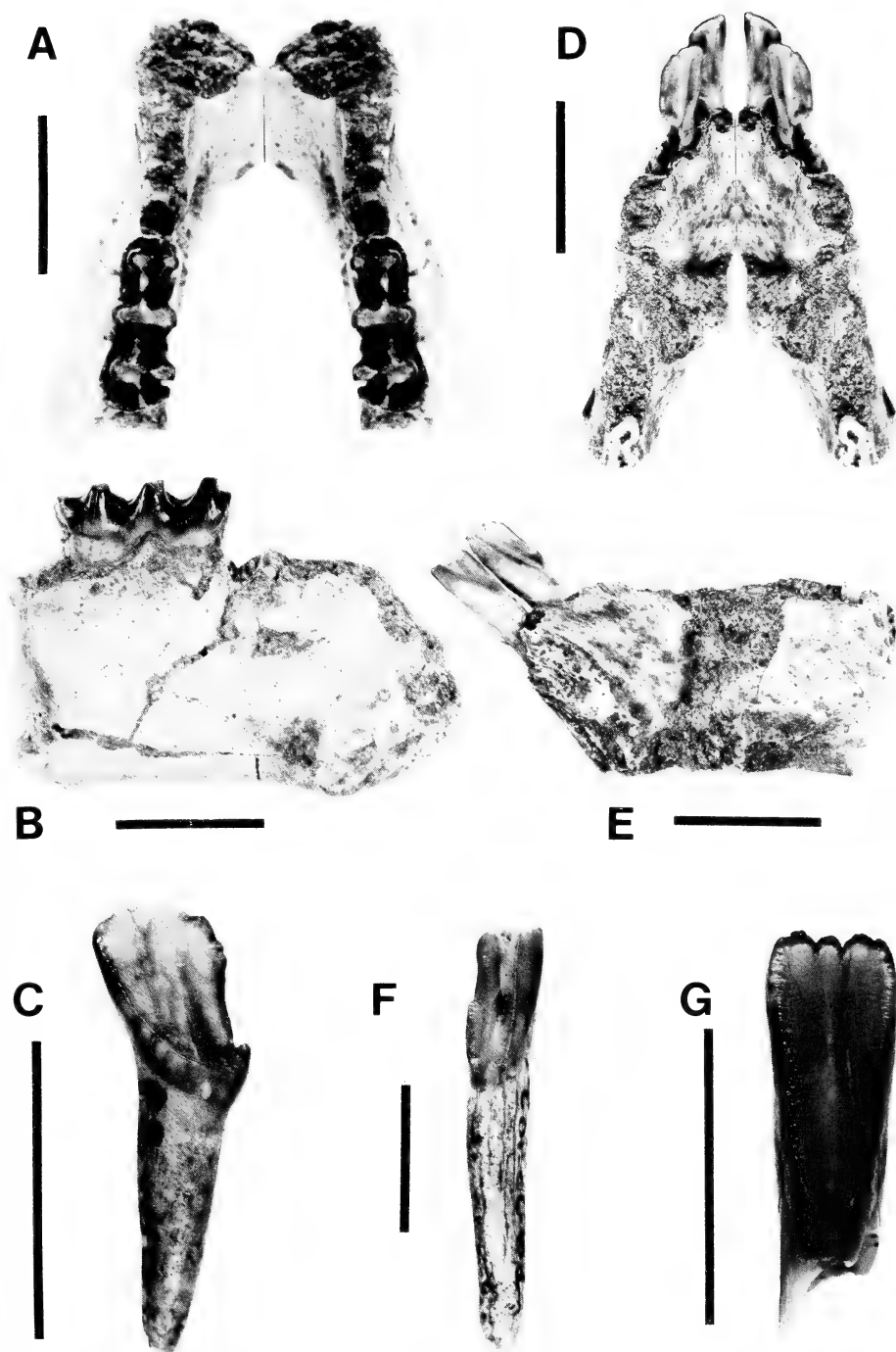


Fig. 2. A-C. *Lopholistriodon moruoroti*. A-B. SAM-PQ-AD2658: juvenile left mandible (with mirror image) containing dm_4 . A. Occlusal view. B. Lingual view. C. SAM-P-AD3015: right I_2 , lingual view.
 D-G. Gen. et sp. indet. D-E. SAM-PQ-AD1697: juvenile right mandible (with mirror image) containing dI_1 - I_2 . D. Occlusal view. E. Lingual view. F. SAM-PQ-AD102d: left I_2 , occlusal view. G. SAM-PQ-AD20d: lower central incisor. Scales = 1 cm.

The I₂ (AD1727) has a distal scoop typical of listriodonts, bordered centrally by a lingual ridge. It has a very light lingual cingulum, but its crown is appreciably longer from cervix to tip than are the corresponding crowns in *L. kidogosana* or species of *Listriodon* (see Pickford 1986).

Remarks

The listriodont fossils from Arrisdrift, Maboko and Moruorot are morphologically and metrically very similar. There can be little doubt that they should be classified in the same species. What is perhaps more difficult to understand is the phyletic position of *Lopholistriodon moruoroti*. It is one of the most derived listriodonts in terms of the perfection of its lophodonty, yet it seems to be one of the earliest known members of the subfamily. It does possess some primitive features, including the retention of a two-rooted P¹ situated close to the canine, and a short diastema. Its precursors are unknown, and there seems little possibility that it was derived from any of the early Miocene East African suids, which are now quite well known (Pickford 1986). The alternative is that they were derived from a small Eurasian precursor—perhaps one of the *Palaeochoerus*-like suids of the early Miocene of Europe—and that they migrated into Africa about 17,5 m.y. ago at the time when many African taxa were translocating to Europe and Asia (Thomas 1985). However, there are no obvious links in the fossil record.

Whatever the case may be, it seems that *Lopholistriodon* was an immigrant to East Africa and South West Africa–Namibia, since there is no sign of listriodont ancestry in the early Miocene deposits of Africa. The presence of *Lopholistriodon* in a fossil fauna is therefore probably good evidence that one is dealing with strata less than 17,5 m.y. old, i.e. middle Miocene rather than early Miocene.

Lopholistriodon kidogosana is known from upper middle Miocene sites in East Africa—such as Ngorora, Kenya—the youngest specimens being about 11 m.y. old. The genus has not yet been found in the same deposits as *Hipparion*, suggesting that, like the genus *Listriodon*, its range was entirely within the middle Miocene period. As such it is a useful genus for broad biostratigraphic correlations.

Family Suidae: gen. et sp. indet.

Figs 2D–G, 3A–C

Material

See Table 2.

Description

Right M³ (AD1795) has marked lingual and buccal flare, and a simple talon, which is little more than a distal cingulum (Fig. 3A). It has a fairly large anterior cingulum and anterior accessory cusp; its main cusps are close together and possess subdued wrinkling, suggestive of the presence of thick enamel.

TABLE 2

Dimensions (in mm) of bunodont suid teeth (gen. et sp. indet.) from Arrisdrift.

<i>Dentition</i>	<i>Specimen</i>	<i>Length</i>	<i>Breadth</i>
Right M ³	AD1795	16,0	13,1
P ⁴ fragment	AD2821	—	9,0
Left I ₁	AD1693	4,3+	4,8
I ₁	AD2355	—	—
Right I ₁	AD20d	4,5	4,7
Left I ₂	AD102d	4,7	5,0
Left mandible with half dM ₄ M ₁ (M ₁)	AD631	11,1	8,9
Right mandible with dI ₁₋₂ (dI ₁)	AD1697	3,1	2,5
(dI ₂)		3,4	2,9

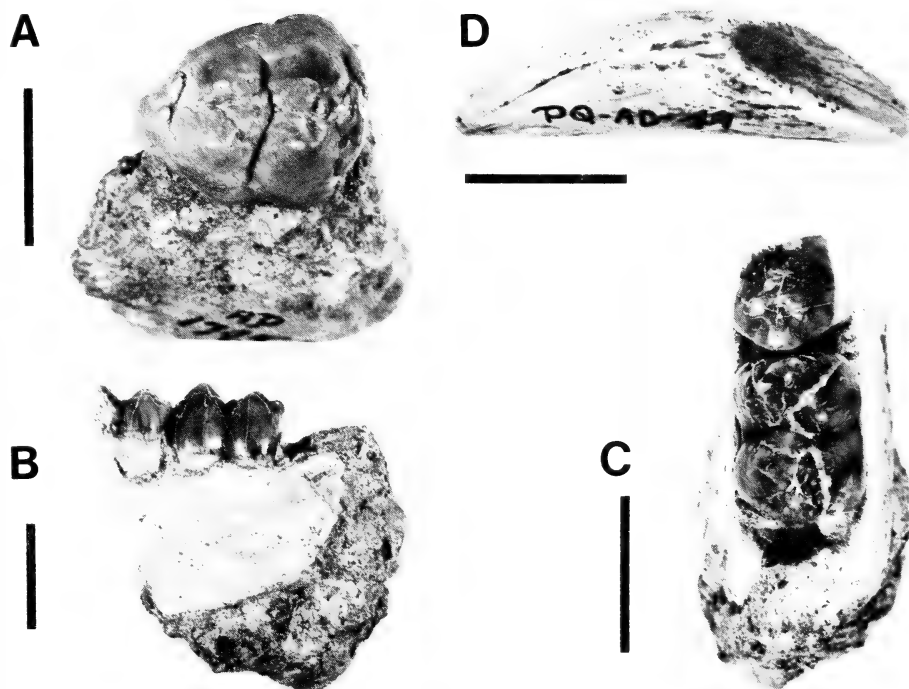


Fig. 3. A-C. Gen. et sp. indet. A. SAM-PQ-AD1795: right M³, occlusal view. B-C. SAM-PQ-AD631: left mandible with half dM₄M₁ (or half M₁-M₂). B. Buccal view. C. Occlusal view.

D. *Lopholistriodon moruoroti*. SAM-PQ-AD49: right upper canine.

Scales = 1 cm.

AD631 (Fig. 3B–C), a juvenile left mandible with a fragment of M_1 and a complete M_2 (or possibly dM_4-M_1), is comparable to *Nguruwe kijivium* in the morphology of its molar crown, although the tooth is higher crowned than is typical of *Nguruwe*.

AD1697 (Fig. 2D–E) is an infant mandible with dI_{1-2} , and alveoli of dI_3-dM_3 . The symphysis, which is complete to the midline, is narrow anteriorly, contrasting with that of *Lopholistriodon*, which is markedly spatulate. The deciduous incisors in the mandible are typically suine, being narrow with concave lingual surfaces bordered by low anterior and posterior ridges. The tip of dI_2 is beaded or crenulated.

AD20d is a rootless, unworn lower central incisor (Fig. 2G), which is pectinate at the tip and which has a central ridge running from crown tip to cervix, as well as mesial and distal lingual ridges.

AD102d is a left I_2 (Fig. 2F), lightly worn with a characteristic distal scoop, lingual rib, and mesial and distal cingular ribs on the lingual side of the crown. The root is long, and in lingual aspect the tooth is gently curved from crown to root, the cervix being more distal than either the root or the crown tips.

Remarks

The eight specimens tentatively assigned to this indeterminate bunodont suid (Table 2) comprise a sample that is insufficient for the purpose of unequivocal identification, bunodonty being a primitive and widespread characteristic of the family. However, the great degree of flare in the upper molars and the lack of buccal and lingual cingula indicate that it is probably not a kubanochoerine, and its affinities possibly lie with genera such as *Palaeochoerus* or *Conohyus*, both of which are well known in Miocene deposits of Europe. More substantial material is required before a positive identification can be made.

POSTCRANIAL BONES

Material

See Table 3.

Remarks

On the basis of their overall sizes, the five postcranial bones from Arrisdrift could belong either to *Lopholistriodon moruoroti* or to the bunodont suid. A decision cannot confidently be made at this time, although—on the basis of quantities of specimens—the chances seem to be higher that they belong to the former rather than the latter. Whatever the final outcome, the available postcranial elements indicate a morphological pattern close to extant suids, from which it is suggested that in its postcranium, the Arrisdrift suid to which these bones belonged was typically suine. Although it was appreciably smaller than any living African suid, the Arrisdrift species was not smaller than the pygmy hog of the Himalaya foothills (*Sus salvinia*).

TABLE 3

Postcranial bones of suid (gen. et sp. indet.) from Arrisdrift (dimensions in mm).

<i>Bone</i>	<i>Specimen</i>	<i>Size</i>
<i>Proximal end left femur</i>	AD3044	
antero-posterior head diameter		15,5
distance from head to greater trochanter		33,3
<i>Complete right tibia</i>	AD2696	
total length		131,2
height of proximal end		22,7
breadth of proximal end		24,5
height of distal end		11,9
breadth of distal end		15,6
<i>Distal end of right tibia</i>	AD646	
height of distal end		11,6
breadth of distal end		15,0
<i>Distal end of metapodial</i>	AD878	
height of distal end		10,5
breadth of distal end		9,5
<i>Distal end of metapodial</i>	AD2711	
height of distal end		9,3
breadth of distal end		8,9

DISCUSSION

The presence of two small suid species at Arrisdrift, in early middle Miocene deposits, is interesting from the point of view of palaeozoogeography, because both may represent immigrants from Eurasia. The subfamily Listriodontinae in particular seems to be absent in lower Miocene deposits of Africa, the only subfamily known in Africa at that time being Kubanochoerinae, which seems to be an unlikely precursor for the listriodonts on a number of morphological grounds (Pickford 1986). On this basis it is suggested that listriodonts migrated into Africa from Eurasia about 17,5 million years ago, and that their origins may be found in the late Oligocene and early Miocene palaeochoerines of Europe.

The bunodont Arrisdrift suid is enigmatic, in that it could represent a peculiar form of kubanochoerine, but I consider it more likely that its affinities lie with the Tetraconodontinae or Palaeochoerinae, both of which are well represented in European deposits of early and middle Miocene age. If this is so then the bunodont Arrisdrift pig would indicate that a second lineage of suids migrated into Africa at the beginning of the early middle Miocene. However, in view of the uncertainty about the identification of this small bunodont pig, it would be unwise to be too dogmatic about this point.

It is probably worth mentioning that isolated teeth have recently been found at Maboko and Nyakach, both of which are early middle Miocene sites in Kenya, which also indicate the probability that Tetraconodontinae were present in Africa

at that time. Unfortunately, none of the specimens is complete enough nor diagnostic enough for the purposes of positive identification, and I prefer to await the discovery of such evidence before using it for biostratigraphic or palaeo-zoogeographic reconstructions.

Suids often seem to have been in the vanguard of major mammal migrations (Ginsberg, Institut de Paléontologie, Paris, pers. comm.), which makes them interesting for reconstructing the sequence and timing of palaeozoogeographic events. It has been suggested on several occasions (Thomas 1985) that initial crossings of the Tethys Seaway occurred about 19 m.y. ago, a period usually referred to as the 'proboscidean datum'. Suids seem not to have partaken in this particular migration, which has been called the first Neogene Dispersal Phase (NDP 1) by Thomas (1985), but undoubtedly reached Africa before it began, indeed earlier than 20 m.y. ago, since they occur at sites such as Legetet and Songhor in Kenya, and Napak in Uganda, all dated about 20 m.y. Indeed the main groups of mammals implicated in the First Dispersal Phase of Thomas are either very large such as proboscideans, were amphibious such as anthracotheres, or were very small such as rodents and insectivores. This peculiar composition of the migrant fauna suggests that a filter was active in restricting the migrations of medium-sized mammals.

In contrast, numerous medium-sized mammals are implicated in Thomas' second Neogene Dispersal Phase (NDP 2), including bovids, hyracoids, tubulidentates, creodonts and suids. These forms are envisaged as having crossed the Tethys region about 17,5 m.y. ago.

It is probable that, as Africa moved northwards due to plate tectonic processes, it approached close enough to Eurasia about 19 m.y. ago to uplift the floor of the Tethys Sea, making it rather shallow in parts, possibly with islands in certain sectors. At this time, filtered migrations of the first Neogene Dispersal Phase would have been possible. As Africa continued moving northwards, parts of the Tethys sea-floor were elevated above sea-level in continuous strips, effectively providing dry-land crossings from Eurasia to Africa. At this time circulation of sea-water between the Atlantic and Indian oceans through the Tethys was severed, which probably had marked effects on local and global climates. The more pervasive migration of mammals in this second Neogene Dispersal Phase dates this event to about 17,5 m.y. Having migrated from Eurasia into Africa, the suids, particularly *Lopholistriodon*, apparently spread quickly throughout the continent, having been found in early middle Miocene sediments in equatorial and southern Africa.

ACKNOWLEDGEMENTS

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- (a) The Figures, Maps and Tables of the paper when referred to in the text
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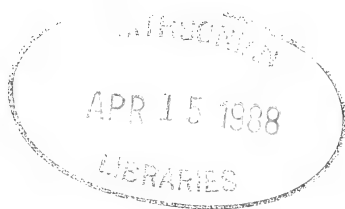
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ANNALS

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FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* 74 (33): 627-634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) 2 (17): 309-320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* 17 (4): 1-51.

THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903-1905* 4 (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* 16: 269-270.

(continued inside back cover)

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A NEW FOSSIL STORK
(AVES, CICONIIDAE) FROM THE
LATE TERTIARY OF LANGEBAANWEG,
SOUTH AFRICA

By
P. J. HAARHOFF

Cape Town Kaapstad

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A NEW FOSSIL STORK (AVES, CICONIIDAE) FROM THE LATE TERTIARY OF LANGEBAANWEG, SOUTH AFRICA

By

P. J. HAARHOFF

*Department of Cenozoic Palaeontology,
South African Museum, Cape Town*

(With 3 figures and 4 tables)

[MS accepted 2 June 1987]

ABSTRACT

A new species of stork, *Ciconia kahli*, from the early Pliocene Varswater Formation, Cape Province, South Africa, is described on the basis of a partial associated skeleton and three other referred specimens. This species has the greatest similarity to the living white stork, *Ciconia ciconia*, but also resembles the saddlebill stork, *Ephippiorhynchus senegalensis*, and black-necked stork, *E. asiaticus*, in certain characters. It is nevertheless very distinctive and probably represents an extinct lineage within the Ciconiidae.

CONTENTS

	PAGE
Introduction	297
Systematics	299
Discussion	310
Acknowledgements	311
References	311

INTRODUCTION

The early Pliocene (c. 5 Ma) Varswater Formation at Langebaanweg, approximately 110 km north-north-west of Cape Town, has yielded a great number and variety of fossils (Hendey 1981*a*, 1981*b*). In a preliminary report on the avian remains from this site Rich (1980) listed a minimum of 61 taxa. Further research on the collection has raised the number of species to 81. Simpson (1971, 1975, 1979) studied the penguin material, which is now being re-examined by Olson (1983, in prep.). Olson (1984) has also described a new species of the ciconiiform family Scopidae, *Scopus xenopus*, and has studied the Procellariiformes (1985*a*) and the ciconiiform family Plataleidae (1985*b*). Rich & Haarhoff (1985) have described a new species of the family Coliidae, *Colius hendeyi*. The associated stork remains described in this paper are from the Quartzose Sand Member (QSM), the lower of the two highly fossiliferous units of the Varswater Formation. This unit accumulated behind a sand-bar in and adjacent to the estuary of the Berg River, which now has a more northerly course. The QSM contains fluviatile, estuarine, floodplain, marsh, tidal mudflat,

and pond facies (Hendey 1976). The partial stork skeleton, SAM-PQ-L22164, was found *in situ*, in the floodplain deposits (QSM 1) of the Quartzose Sand Member. Three other bones of uncertain provenance have been referred to the same species.

Kahl's (1972) classification of living storks is followed here (Table 1), although it requires revision (see p. 310). Comparisons with living species indicate that, on the basis of the premaxilla and mandible, the fossil stork belongs to the tribe Ciconiini. The postcranial material is sufficiently different from all the living species and all known fossil species to warrant assignment to a new species. The new fossil stork does bear certain resemblances to *Ciconia ciconia* and to a lesser extent to *Ephippiorhynchus senegalensis* and *E. asiaticus*.

The material described is housed in the Department of Cenozoic Palaeontology, South African Museum. Catalogue numbers of fossil material are prefixed SAM-PQ, with the additional prefix L indicating material from Lange-

TABLE 1
Classification of the Ciconiidae according to Kahl (1972).

Family Ciconiidae	
Tribe Mycteriini	
<i>Mycteria americana</i> Linnaeus	American wood stork
<i>Mycteria cinerea</i> (Raffles)	milky stork
<i>Mycteria ibis</i> (Linnaeus)	yellowbilled stork
<i>Mycteria leucocephala</i> (Pennant)	painted stork
<i>Anastomus oscitans</i> (Boddaert)	Asian openbill stork
<i>Anastomus lamelligerus</i> Temminck	African openbill stork
<i>A. l. lamelligerus</i> Temminck	
<i>A. l. madagascariensis</i> Milne Edwards	
Tribe Ciconiini	
<i>Ciconia nigra</i> (Linnaeus)	black stork
<i>Ciconia abdimii</i> Lichtenstein	Abdim's stork
<i>Ciconia episcopus</i> (Boddaert)	woollynecked stork
<i>C. e. episcopus</i> (Boddaert)	
<i>C. e. microscelis</i> G. R. Gray	
<i>C. e. stormi</i> (Blasius)*	
<i>Ciconia maguari</i> (Gmelin)	maguari stork
<i>Ciconia ciconia</i> (Linnaeus)	white stork
<i>C. c. ciconia</i> (Linnaeus)	
<i>C. c. asiatica</i> Severtzov	
<i>C. c. boyciana</i> Swinhoe*	
Tribe Leptoptilini	
<i>Ephippiorhynchus asiaticus</i> (Latham)	blacknecked stork
<i>E. a. asiaticus</i> (Latham)	
<i>E. a. australis</i> (Shaw)	
<i>Ephippiorhynchus senegalensis</i> (Shaw)	saddlebill stork
<i>Jabiru mycteria</i> (Lichtenstein)	jabiru stork
<i>Leptoptilos javanicus</i> (Horsfield)	lesser adjutant stork
<i>Leptoptilos dubius</i> (Gmelin)	greater adjutant stork
<i>Leptoptilos crumeniferus</i> (Lesson)	marabou stork

*Possibly has attained specific status; further study needed.

baanweg. Modern comparative material in the South African Museum is distinguished by the prefix SAM-ZO.

Institutional abbreviations used in the text are as follows:

AMNH	American Museum of Natural History, New York.
AM-S	Australian Museum, Sydney.
ANWC	Australian National Wildlife Collection, Canberra, Australia (CSIRO).
BMNH	British Museum (Natural History), London.
LACM	Natural History Museum of Los Angeles County, California.
NMV	National Museum of Victoria, Australia.
OT-B	Otago Museum, Dunedin, New Zealand.
SAM	South African Museum, Cape Town.
TM	Transvaal Museum, Pretoria.
UCMP	University of California, Museum of Paleontology, Berkeley.

Most measurements (in mm) were taken following Von den Driesch (1976) and Olson (1985*b*). Anatomical terminology follows that of Howard (1929).

Comparative material examined

Mycteria americana, SAM-ZO57920; *M. leucocephala*, BMNH 396A, BMNH 396B; *M. ibis*, AM-S 1235; *Anastomus lamelligerus*, TM 33382, AMNH 5292; *Ciconia nigra*, SAM-ZO56944, OT-B76:1; *C. abdimii*, TM 33336; *C. episcopus*, TM 33391; *C. maguari*, AM-S 551; *C. ciconia*, SAM-ZO56181, SAM-ZO57363, SAM-ZO57471, AM-S 1126; *Ephippiorhynchus asiaticus*, BMNH 955B, ANWC 108, ANWC 686, ANWC 4139, ANWC 1508, NMV-B6753; *E. senegalensis*, LACM 90275, AMNH 2903; *Leptoptilos dubius*, NMV-B11426, NMV-R2203, NMV-W5083; *L. crumeniferus*, TM 33412; *L. javanicus*, NMV-B736, AMNH 5059; *Jabiru mycteria*, AMNH 2659, UCMP 133932.

SYSTEMATICS

Family Ciconiidae Gray, 1840

The fossil specimens can be referred to the Ciconiidae on the basis of the following characters: (1) sternum excavated on anterior carinal margin; (2) last thoracic vertebra not fused to synsacrum; (3) synsacrum, cranial view, prezygapophysis not joined to diapophysis at posterior edge; (4) scapular facet of coracoid deep and well rounded; (5) carpal tuberosity of ulna pointed, with ligamental attachment on caudal surface; (6) intercotylar prominence on tarsometatarsus rises well above cotylae, which are more or less of equal height; and (7) trochleae II and IV rather flattened anteriorly, not rounded. Characters 1, 4, 5, 6, and 7 separate the Ciconiidae from the Scopidae, Ardeidae and Plataleidae, character 2 from the Scopidae, and character 3 from the Ardeidae and Plataleidae.

Genus *Ciconia* Brisson, 1760

The fossil species described below is referable to the genus *Ciconia* by having the combination of: (1) tips of maxilla and mandible straight; (2) anterior carinal margin of sternum unperforated; (3) coracoid with a ridge between head and midpoint of shaft in ventral view; (4) deep depression between the proximal articulating surface of the tarsometatarsus and the hypotarsus; and (5) lack of significantly pneumatic postcranial elements.

Characters 1–5 distinguish the genus *Ciconia* from the other five Recent genera of Kahl (1972) and therefore the following putative extinct species within those genera: *Mycteria wetmorei* Howard, 1935; *Leptoptilos falconeri* (Davies, 1880) (Lydekker 1884; Harrison 1974); *L. siwalikensis* Harrison, 1974; *L. richae* (Harrison, 1974); *L. titan* Wetmore, 1940; *L. pliogenicus* Zubareva, 1948; *Leptoptilos* sp. Hill & Walker, 1979; *Ephippiorhynchus pakistanensis* Harrison & Walker, 1982.

The fossils from Langebaanweg were also compared with and found to be distinct from the following extinct genera: *Palaeoephippiorhynchus dietrichi* Lambrecht, 1930; *Grallavis edwardsi* (Lydekker, 1891) (Lambrecht 1933; Cheneval 1984); '*Propelargus*' *olseni* Brodkorb, 1963 (requires revision, Cheneval pers. comm.); '*Dissouroides*' *milleri* Short, 1966 (requires revision, Olson pers. comm.); *Cryptociconia indica* Harrison, 1974; *Pelargosteon tothi* Kretzoi, 1962; '*Prociconia*' *lydekkeri* Ameghino, 1891 (requires revision, Olson pers. comm.). *Ciconiopsis antarctica* Ameghino, 1899, was not studied by the author but, since it is from the early Oligocene of Argentina, it seems unlikely that the fossils from Langebaanweg should be assigned to this genus. Also, according to Olson (1986), it requires restudy before it can be accepted as a stork.

Ciconia kahli sp. nov.

Figs 1–3

Material

Holotype. SAM-PQ-L22164, partial associated skeleton consisting of the following elements: fragment of premaxilla (length 53,7 mm), mandibular symphysis (length 80,7 mm) plus associated fragments; part of sternal manubrium and coracoidal sulcus; complete furcular process plus fragmented pieces; complete left proximal and incomplete right proximal scapulae; incomplete left and right coracoids; incomplete left distal humerus; fragments of head, shaft, and distal end of right humerus; almost complete right ulna; external cotyla and crushed fragments of shaft of left ulna; complete right radius (slightly damaged proximal end); right scapholunar; right cuneiform; right carpometacarpus; right phalanx 1 and 2 of major alar digit; incomplete right femur; incomplete distal end of left tibiotarsus and shaft; incomplete right fibula; incomplete left tarsometatarsus (lacks distal end); pes—incomplete ungual phalanx, possibly of digit 3; first and second thoracic vertebrae; eleventh and twelfth cervical vertebrae (pathological), plus numerous vertebral fragments.

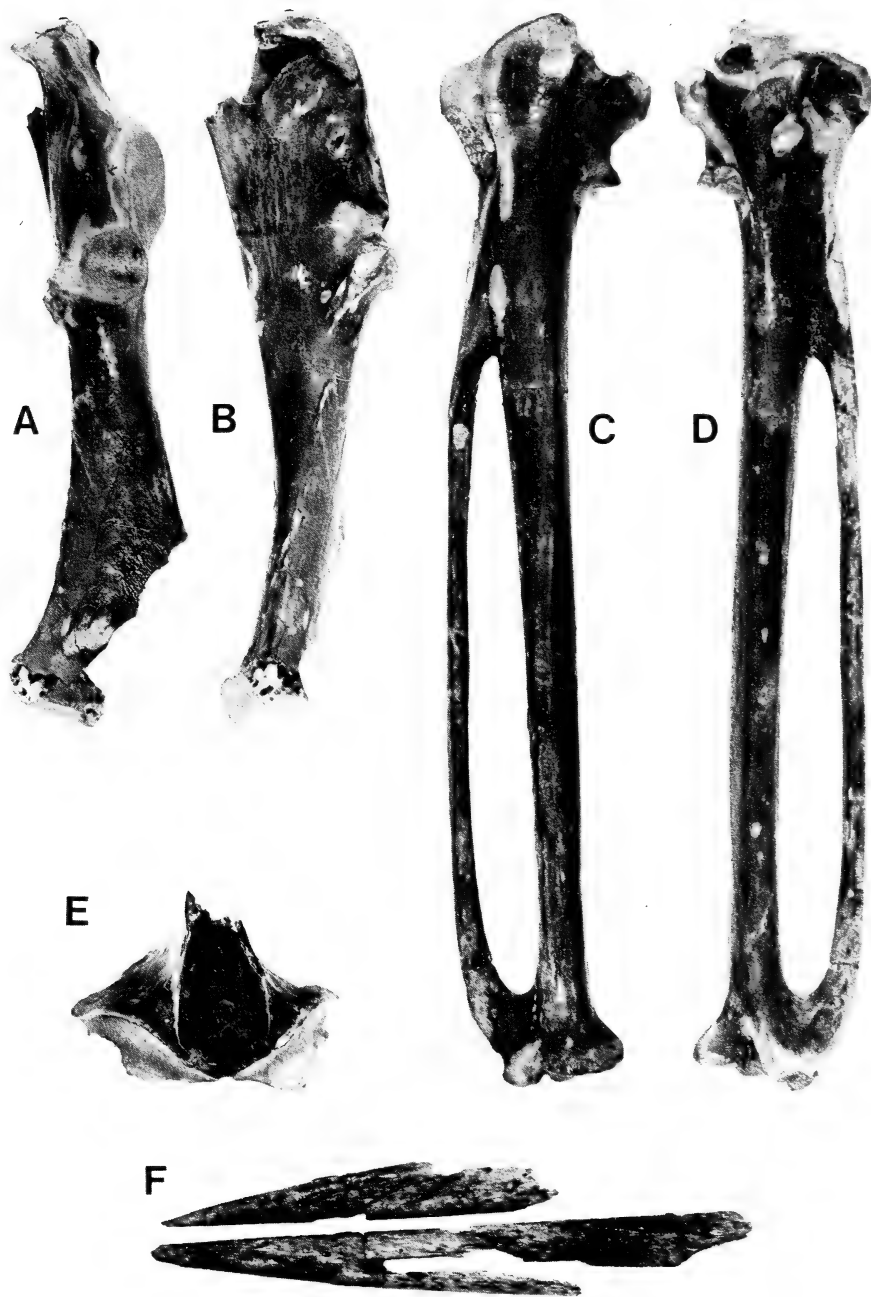


Fig. 1. *Ciconia kahli* sp. nov., holotype, SAM-PQ-L22164. A-B. Coracoid. C-D. Carpometacarpus. E. Sternum. F. Maxilla and mandible. All $\times 1$.

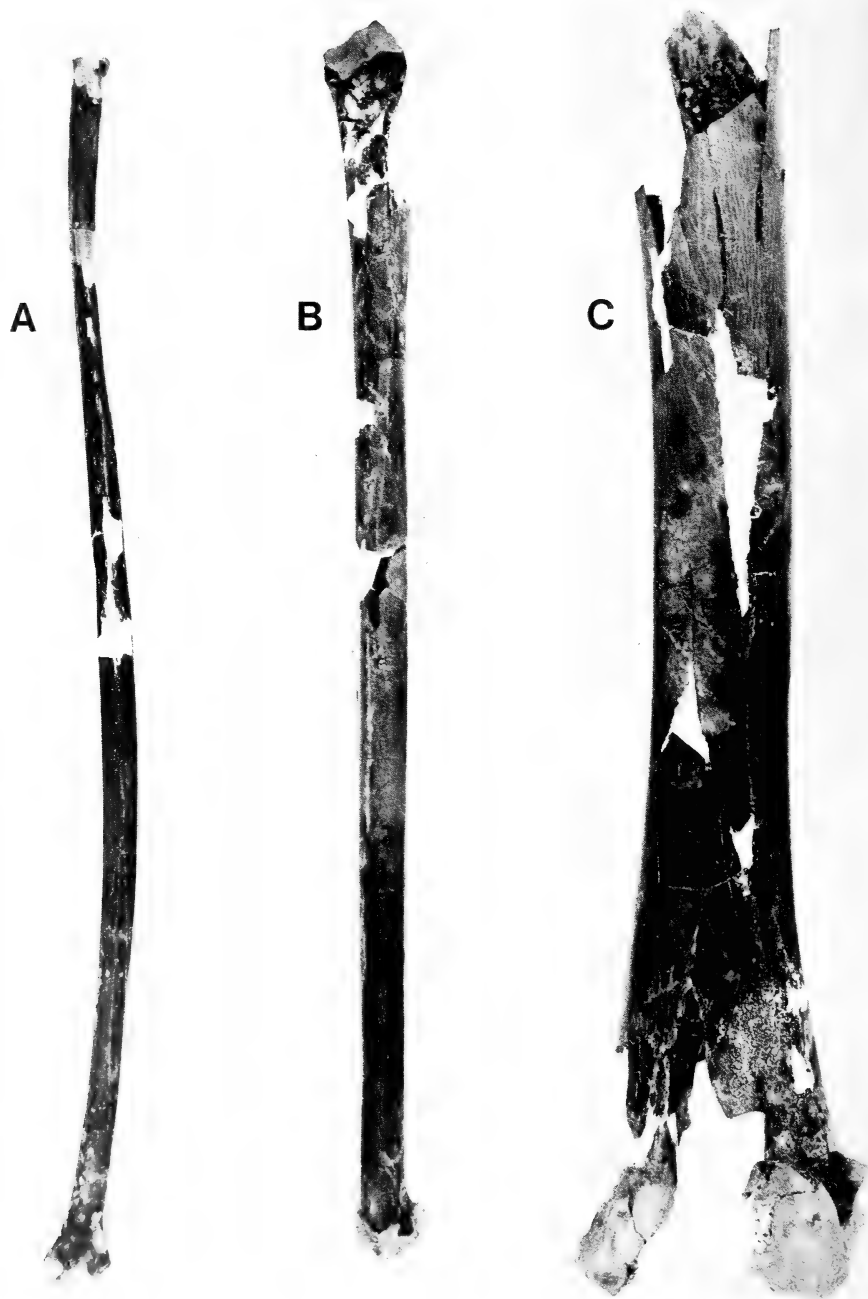


Fig. 2. *Ciconia kahli* sp. nov., holotype, SAM-PQ-L22164. A. Radius. B. Ulna. C. Humerus. D. Proximal end of humerus. E. Humerus (proximal view). F. Distal end of tibiotarsus (internal view). G. Femur (posterior view). H. Femur (internal view). I. Tibiotarsus. A-B. $\times 0,5$. C-H. $\times 1$. I. $\times 0,6$.

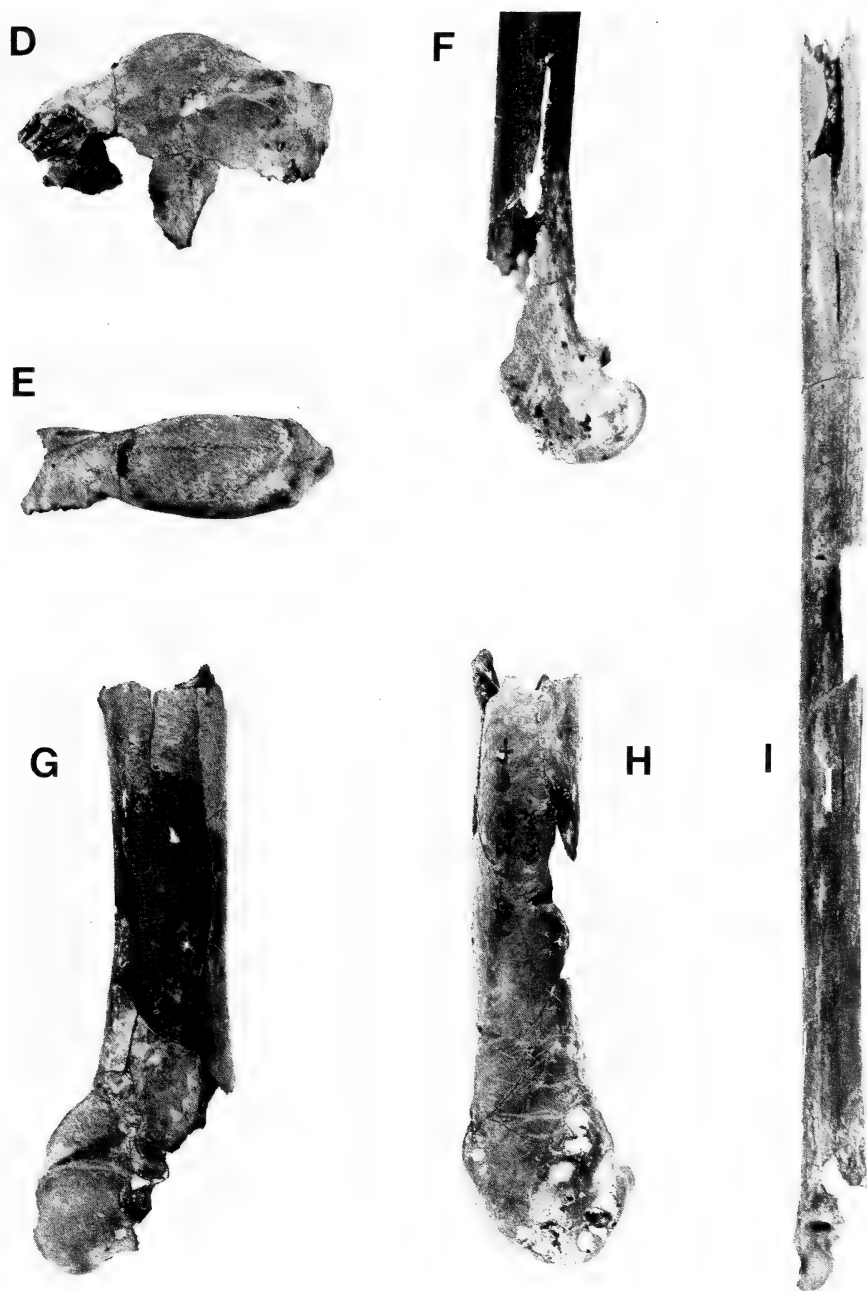


Fig. 2 (contd)

Paratypes. SAM-PQ-L41955, synsacrum lacking a few caudal vertebrae. SAM-PQ-L42157, right ulna lacking proximal end. SAM-PQ-L-6508, complete distal end of right tarsometatarsus (Fig. 3). Including the holotype, the minimum number of individuals is two.

Measurements of holotype (in mm)

Humerus: actual length, 180,0; estimated greatest length, 274,0; estimated distal width, 41,2; smallest width of shaft, 19,1. Ulna: actual length of proximal portion, 133,4; actual length of distal portion, 183,0; estimated greatest length, 320,0; greatest diagonal of distal end, 20,9; smallest width of shaft, 9,5. Radius: greatest length, 304,0; least and greatest diameter of shaft at midpoint, $5,1 \times 8,7$; greatest distal diameter, 18,4. Carpometacarpus: greatest length, 144,3; depth through process of metacarpal 1, 29,0; greatest proximal width through trochleae, 12,6; width and depth of major metacarpal at midpoint, $9,7 \times 6,9$; greatest distal diameter, 16,3. Coracoid: medial length, 93,4; estimated greatest length, 103,0; greatest depth of sternal facet, 12,6. Sternum: greatest width of excavation on anterior carinal margin, 12,0; greatest breadth of coracoidal sulcus, 14,1. Scapula: greatest cranial diagonal, 26,6. Femur: actual length, 32,5; estimated greatest length, 117,9; approximate shaft width and depth, $15,2 \times 15,4$. Tibiotarsus: actual length, 267,7; estimated greatest length, 348,0; width and depth of shaft at approximate midpoint, $14,6 \times 11,2$; depth of anterior internal condyle, 13,8; length of supratendinal bridge, 6,3. Fibula: actual length, 51,4; estimated greatest length, 230,0. Tarsometatarsus: actual length, 292,1; estimated greatest length, 321,7; proximal width, 22,5; approximate width and depth of shaft at approximate midpoint, $9,7 \times 9,4$.

Measurements of paratypes (in mm)

Synsacrum, SAM-PQ-L41955: actual length, 96,1; depth at midpoint of second synsacral thoracic vertebra, 36,4; width of first synsacral thoracic vertebra at midpoint, 7,4. Ulna, SAM-PQ-L42157: actual length, 158,6; greatest diagonal of distal end, 20,9. Tarsometatarsus, SAM-PQ-L6508: distal width, 24,5; width and depth of middle trochlea, $7,9 \times 11,7$.

Diagnosis

Larger than all five extant species of *Ciconia* (Table 2) and the extinct species *Ciconia minor* Harrison, 1980, *Ciconia sarmatica* Grigorescu & Kessler, 1977, and *Ciconia nana* (De Vis, 1888) (Rich & Van Tets 1982). Also larger than *Ciconia* sp. Harrison, 1980, and *Ciconia* sp. Ono, 1984. *Ciconia* sp. Stehlin, 1923, is juvenile and was not considered. Smaller than *Ciconia gaudryi* Lambrecht, 1933. Within size range (Table 3) of the extinct species *Ciconia maltha* Miller, 1910, but morphologically distinct as follows: sternum—excavation on anterior carinal margin shallower and wider; coracoid—internal view, less inflated below depression beneath brachial tuberosity and brachial tuberosity less erect; humerus—shaft more robust (see also unique features below);

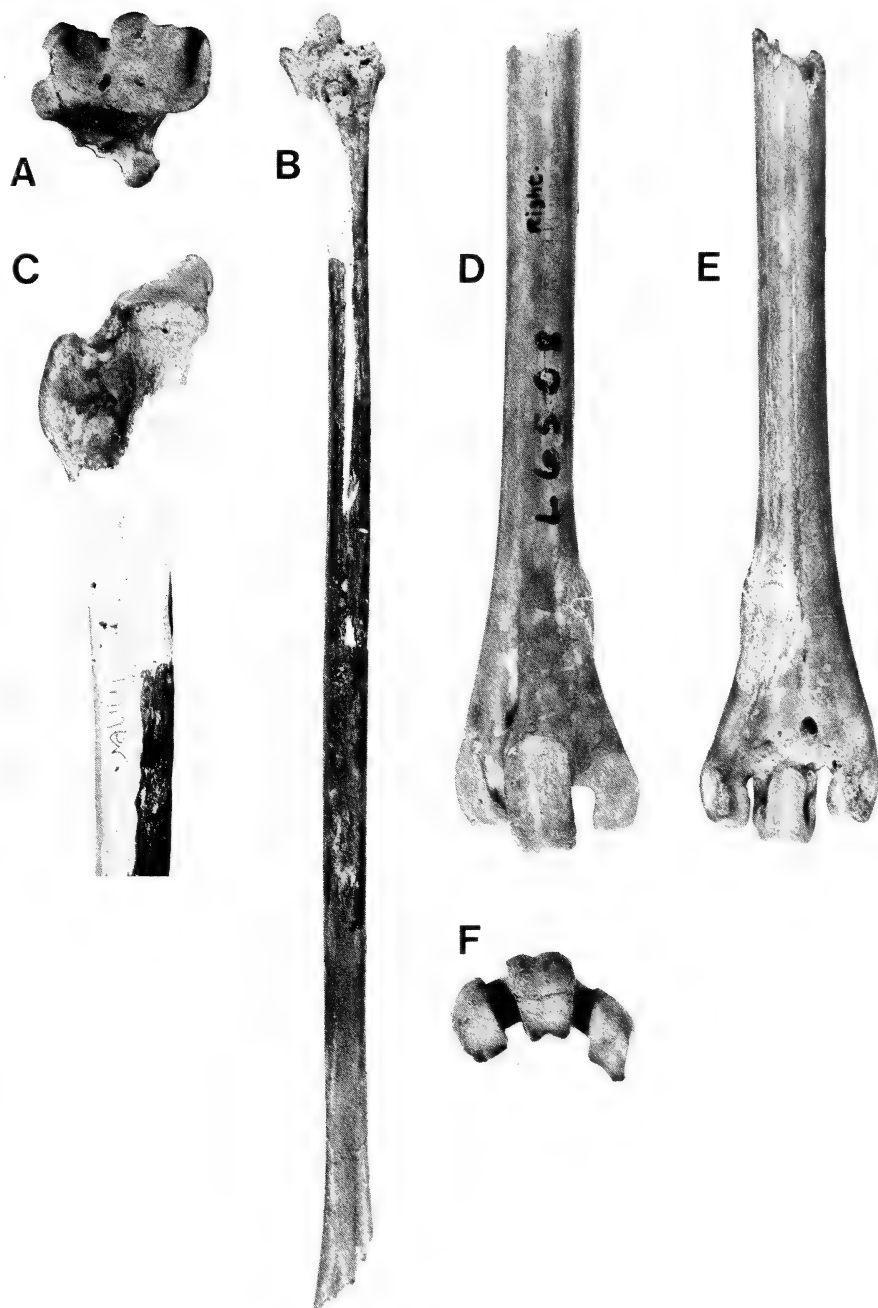


Fig. 3. *Ciconia kahli* sp. nov. A-C. Holotype, SAM-PQ-L22164. Tarsometatarsus. A. Proximal view. B. Anterior view. C. Internal view. D-F. Paratype, SAM-PQ-L6508. Tarsometatarsus. D. Anterior view. E. Posterior view. F. Distal view. A, C-F. $\times 1$. B. $\times 0,6$.

TABLE 2

Length measurements (mm) of major elements of *Ciconia kahli* sp. nov. compared with extant species of *Ciconia*.

	<i>C. kahli</i> (n = 1)	<i>C. nigra</i> (n = 2)	<i>C. abdimii</i> (n = 1)	<i>C. episcopus</i> (n = 1)	<i>C. maguari</i> (n = 1)	<i>C. ciconia</i> (n = 4)
Coracoid	103*	77,5–85,5	63,5	66,4	97,9	80,5–90,9
Humerus	274*	191,4–197,1	151,7	158,1	223,5	196,8–213,8
Ulna	320*	218,4–230,9	174,0	185,7	265,4	227,1–253,0
Radius	304	209,4–220,0	166,3	179,0	254,3	216,1–242,8
Carpometacarpus	144,3	110,7–113,5	84,0	85,4	119,5	107,7–114,6
Femur	117,9*	94,5–94,8	71,6	73,9	113,0	90,1–110,7
Tibiotarsus	348*	239,1–246,6	177,6	202,6	311,4	238,2–260,8
Tarsometatarsus	321,7*	192,4–200,1	133,5	150,2	272,4	198,1–225,1

* = estimated

tarsometatarsus—intercotylar prominence narrower, in distal view trochleae less arched and trochlea III less raised and rounded in external view in *C. kahli*.

Ciconia kahli differs morphologically from the extant species of *Ciconia* as follows: sternum—expanded coracoidal sulcus; coracoid—neck proportionally longer; radius—shaft less curved; carpometacarpus—inner carpal trochlea, internal view, flattened anteriorly; tibiotarsus—internal ligamental prominence placed further away from internal margin; tarsometatarsus—depression between hypotarsus and proximal articulating surface deeper in *C. kahli*.

Certain features of the humerus of *C. kahli* are different from all species of Ciconiidae studied for this report: (1) head, palmar view, relatively flattened, sloping gradually toward external side; (2) proximal view, head broader near external tuberosity; (3) capital groove shallow; (4) groove between ectepicondylar prominence and external condyle deep.

Distribution

Early Pliocene Varswater Formation (Quartzose Sand Member Unit I and possibly Pelletal Phosphorite Member bed 3aS) at Langebaanweg, south-western Cape Province, South Africa.

Etymology

This species is named in honour of Dr M. Philip Kahl, who has done so much work on the Recent genera of the family Ciconiidae.

Remarks

Although *Ciconia kahli* has the greatest similarity to *C. ciconia*, it shares the following characters with *Ephippiorhynchus*: (1) twelfth cervical vertebra not longitudinally compressed; (2) first and second thoracic vertebrae with hypapophyses; (3) ulna, in palmar view, flattened immediately below the proximal radial depression; (4) carpometacarpus, in internal view, with a deep depression between metacarpal I and the pisiform process; (5) internal condyle of tibiotarsus,

TABLE 3
Comparative measurements (mm) for fossil species of *Ciconia* and *Ciconia kahl* sp. nov.

	<i>Ciconia</i> sp. ¹	<i>Ciconia</i> <i>minor</i> ²	Kenya	Kenya	<i>Ciconia</i> sp. ²	<i>Ciconia</i> <i>gaudryi</i> ³	<i>Ciconia</i> <i>nana</i> ⁴ (n = 2)	<i>Ciconia</i> <i>maltha</i> ⁵	<i>Ciconia</i> <i>sarmatica</i> ⁶	<i>Ciconia</i> <i>kahl</i> ⁴
	Japan	Kenya	Kenya	Kenya	Greece	Australia	California Florida Oregon Idaho	Romania	South Africa	
Scapula										
Humerus										
Ulna					310					
Carpometacarpus										
gl										
bp										
Carocoid										
Femur										
gl										
gl										
bd										
Tibiotarsus										
lsb										
gl										
daic										
bd										
Tarsometatarsus										
gl	200*									
bp										
bd										

* = estimated; bp = proximal breadth; gl = greatest length; bd = distal breadth; lsb = length of supratendinal bridge; daic = depth of anterior internal condyle. References: 1. Ono 1984. 2. Harrison 1980. 3. Lambrecht 1933. 4. Present study. 5. Howard 1942. 6. Grigorescu & Kessler 1977.

TABLE 4
Age and distribution of all fossil and living storks studied for this report.

	NEARCTIC	NEO-TROPICAL	PALEARCTIC	ETHIOPIAN	ORIENTAL	AUSTRALASIAN
HISTORIC	<i>Mycteria americana</i>	<i>Mycteria americana</i> <i>Ciconia maguari</i> <i>Jabiru mycteria</i>	<i>Ciconia nigra</i> <i>Ciconia ciconia</i>	<i>Mycteria ibis</i> <i>Anastomus lamelligerus</i> <i>Ciconia nigra</i> <i>Ciconia abdimii</i> <i>Ciconia episcopus</i> <i>Ciconia ciconia</i> <i>Ephippiorhynchus senegalensis</i> <i>Leptoptilos crumeniferus</i>	<i>Mycteria cinerea</i> <i>Mycteria leucocephala</i> <i>Anastomus oscitans</i> <i>Ciconia episcopus</i> <i>Ciconia nigra</i> <i>Ciconia ciconia</i> <i>Ephippiorhynchus asiaticus</i> <i>Leptoptilos javanicus</i> <i>Leptoptilos dubius</i>	<i>Ciconia episcopus</i> <i>Ephippiorhynchus asiaticus</i>
LATE	<i>Mycteria americana</i> <i>Mycteria wetmorei</i> <i>Ciconia maltha</i>	<i>Ciconia maguari</i> <i>Jabiru mycteria</i> (0,14) ¹ <i>Mycteria americana</i> (0,14) ¹ ' <i>Procionia</i> ' <i>lydekkeri</i>	<i>Ciconia ciconia</i> <i>Ciconia nigra</i> <i>Mycteria (Ibis) ibis</i>			<i>Ciconia nana</i>
PLEISTOCENE						
EARLY						
			<i>Pelargosteon tothi</i> <i>Ciconia sp.</i>			

PLIOCENE	LATE	<i>Ciconia maltha</i> (3,4 + 0,27) ²	<i>Leptoptilos</i> <i>siwalikensis</i> (1,8–3,0) ^{3,4} <i>Leptoptilos</i> <i>falconeri</i> (1,8–3,0) ^{3,4} <i>Cryptociconia</i> <i>indica</i> (1,8–3,0) ^{3,4}
MIOCENE	MIDDLE		<i>Leptoptilos</i> <i>pliocenicus</i>
	EARLY	' <i>Dissouroides</i> ' <i>milleri</i>	<i>Ciconia kahl</i> sp. nov. (5,0) ⁵ <i>Ciconia gaudryi</i> (9,0) ³ <i>Leptoptilos richae</i> <i>Ciconia sarmatica</i> (12,0) ⁸
	LATE		<i>Ephippiorhynchus</i> <i>pakistanensis</i> <i>Leptoptilos</i> <i>siwalikensis</i> *
	MIDDLE	' <i>Propelargus</i> ' <i>olseni</i> (13,5–15,0) ⁹	<i>Ciconia</i> sp.
	EARLY		<i>Grallavis edwardsi</i> <i>Ciconia minor</i>
OLIGOCENE	EARLY	' <i>Ciconiopsis</i> ' <i>antarctica</i>	<i>Palaeoepphippio-</i> <i>rhynchus</i> <i>dietrichi</i>

Where possible, dates in million of years before present have been given in parentheses. References: 1. Campbell 1979. 2. Feduccia 1967. 3. Berggren & Van Couvering 1974. 4. Harrison (pers. comm.). 5. Henney 1981a, 1981b. 6. Archer & Wade 1976. 7. Hill & Walker 1979. 8. Grigorescu & Kessler 1977. 9. Blackwelder 1980. *Tentatively referred specimen—Harrison & Walker 1982.

in distal view, with convex external margin; (6) depression between hypotarsus and proximal articulating surface; (7) trochleae, in distal view, form fairly flat, wide, arch; (8) similar shape of trochlea III and position of trochlea IV.

Proportional differences observed include the following: (1) *Leptoptilos* (apart from *L. javanicus*) is the only genus in which the ulna is longer than the tibiotarsus. *Ephippiorhynchus* is extreme in that the tibiotarsus is considerably longer than the ulna. In the relative length of the ulna and tibiotarsus, *C. kahli* is more similar to the *Ciconia* group and *Jabiru mycteria*. (2) *Ciconia kahli* differs from Recent storks in having the tarsometatarsus and tibiotarsus about equal in length, whereas in all other species the tibiotarsus is longer, especially so in *Leptoptilos crumeniferus*, *L. dubius*, and *Mycteria leucocephala*.

DISCUSSION

Wood (1984) suggested from his phenetic analysis, based on major skeletal elements of the stork, that *Jabiru mycteria* be included in the genus *Ephippiorhynchus* and that *Ephippiorhynchus* should be transferred to the tribe Ciconiini. Observations in this report on the similarities between *Ciconia* and *Ephippiorhynchus* support this view. Also, on the basis of their comparisons of the genetic material, DNA, Sibley & Ahlquist (1985) place *Ciconia* and *Ephippiorhynchus* on the same branch of their phylogram. However, Cheneval (1984) found that, although the fossil stork *Grallavis edwardsi* is most closely related to *Ephippiorhynchus*, it also has some characters in common with *Leptoptilos*, so the fossil record may require some revision of Kahl's (1972) classification.

Ciconia kahli was a tall, fairly robust bird with shorter wings but longer legs than *Leptoptilos crumeniferus*. Its most distinctive features are in the humerus, radius, carpometacarpus, tibiotarsus and tarsometatarsus. Olson (pers. comm.) has pointed out that the greater size of *C. kahli* is paralleled by some of the Pliocene and Pleistocene species of *Leptoptilos* that were much larger than any modern species of that genus. As shown in Table 4, *Ciconia* is the most common and widespread genus of stork in Tertiary and Historic times. Just how the species of *Ciconia* are related to one another is as yet undetermined, but *Ciconia kahli* seems sufficiently distinct morphologically as not to have been ancestral to any living species and thus may represent an extinct lineage within the Ciconiidae.

Two species of stork occur today in the southern and south-western Cape Province of South Africa. They are *Ciconia c. ciconia* and *C. nigra*. Neither is common in the Langebaanweg area. *Ciconia c. ciconia* is a Palearctic migrant, although a few pairs breed in the southern Cape. *Ciconia nigra* is a locally migratory species recorded as breeding in the eastern and southern Cape (Clancey 1980).

The inferred habitat (floodplain close to a river with marshy areas) is in keeping with that preferred by some contemporary species of the family Ciconi-

dae. Others, including *C. ciconia*, are opportunistic and take advantage of fires and burned areas. This could have been true of the Langebaanweg stork, for such conditions were also present at the time of deposition (Hendey 1981*b*).

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Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

P. J. HAARHOFF

A NEW FOSSIL STORK (AVES, CICONIIDAE)
FROM THE LATE TERTIARY OF
LANGEBAANWEG, SOUTH AFRICA

VOLUME 97 PART 12

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A REDESCRIPTION OF THE SOFT CORAL
ALCYONIUM VALDIVIAE KÜKENTHAL, 1906,
WITH THE DESCRIPTION OF A NEW
SPECIES OF *LITOPHYTON* FORSKÅL, 1775,
FROM SOUTHERN AFRICA
(OCTOCORALLIA, ALCYONACEA)

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A REDESCRIPTION OF THE SOFT CORAL *ALCYONIUM VALDIVIAE*
KÜKENTHAL, 1906, WITH THE DESCRIPTION OF A NEW SPECIES OF
LITOPHYTON FORSKÅL, 1775, FROM SOUTHERN AFRICA
(OCTOCORALLIA, ALCYONACEA)

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(With 8 figures)

[MS accepted 1 December 1987]

ABSTRACT

Two presumably endemic species of soft corals are described from the shallow sublittoral of southern Africa. A redescription of *Alcyonium valdiviae* Kükenthal, 1906 (family Alcyoniidae), is presented, with a brief assessment of its variability, as well as a comparison with related southern African taxa. Previous authors have confused this species with *Cladiella pachyclados* (Klunzinger, 1877). The present re-evaluation, based on recently collected material, confirms that *C. pachyclados* is not part of the fauna of the south coast of South Africa.

A recently discovered species of the genus *Litophyton* Forskål, 1775 (family Nephtheidae), is here described as *Litophyton liltvedi* sp. nov., and is compared with other sympatric and superficially similar species. This description represents the first record of the genus for the subcontinent.

CONTENTS

	PAGE
Introduction	315
Systematic account	316
Acknowledgements	328
References	328

INTRODUCTION

Recent exploration of the shallow sublittoral of South Africa by means of SCUBA and dredge has yielded many new species and records of soft corals as well as newly acquired material of many previously described species that have not been collected for the past 60-90 years.

From Dr G. C. Williams, Curator of Lower Invertebrates, South African Museum, Cape Town, Dr J. Verseveldt received some alcyonacean specimens for examination. Among these were five colonies of a soft coral, similar specimens of

* Deceased, manuscript published posthumously.

which were previously identified as *Alcyonium pachyclados* Klunzinger, 1877, by Hickson (1900: 72) and J. Stuart Thomson (1910: 570; 1921: 50). The generic designation for *A. pachyclados* is now recognized as *Cladiella* Gray, 1869, based on the form and distribution of sclerites (Tixier-Durivault 1966: 50). It was found that the recently collected material mentioned above is conspecific with *Alcyonium valdiviae* Kükenthal, 1906.

Another colony received represents a new species of *Litophyton* Forskål, 1775, an Indo-Pacific genus previously unrecorded from the coasts of southern Africa.

Since the death of Dr Verseveldt on 29 March 1987 precluded the possibility of the referees' comments being incorporated into the original manuscript, Dr J. C. den Hartog (Curator of Coelenterata at the Rijksmuseum van Natuurlijke Historie, Leiden), long-time associate and friend of Dr Verseveldt, suggested that Dr Williams make the necessary revisions of the manuscript and act as co-author. This has been effected, together with the redrawing of the figures portraying the polyps and sclerites, and the inclusion of scanning electron micrographs as well as a map showing the geographic distribution of the two species.

SYSTEMATIC ACCOUNT

Family **Alcyoniidae** Lamouroux, 1812

Alcyonium Linnaeus, 1758

Alcyonium valdiviae Kükenthal, 1906

Figs 1, 2A, C-E, 3

Alcyonium valdiviae Kükenthal, 1906: 42, pl. 3 (fig. 11), pl. 8 (figs 39-41).

Alcyonium pachyclados (*non* Klunzinger, 1877): Hickson, 1900: 72. J. Stuart Thomson, 1910: 570, pl. 2 (fig. 14), pl. 4 (figs 33, 34); 1921: 155-156, pl. 5 (figs 6-8).

Material

SAM-H3347, 1 colony (Fig. 1A, B), reef 2 km off Bird Rock, Algoa Bay, 33°50'S 25°40'E, depth 15 m, SCUBA, 17 May 1984, coll. G. C. Williams. SAM-H3661, 1 colony, Gonubie, Eastern Cape Province, Station XX38, 32°51,2'S 28°02,8'E, depth 30 m, dredge, 17 July 1981, coll. G. C. Williams (RV *Meiring Naude*). SAM-H3384, 1 colony (Fig. 1D), off Gans Bay, Western Cape Province, 34°36,6'S 19°12,6'E, depth 78 m, 11 October 1983, coll. Sea Fisheries Research Institute. SAM-H3732, 1 colony (Fig. 1C), Hottentots Huisie, Cape Peninsula, 33°59'S 18°21'E, depth 14 m, SCUBA, 22 March 1984, coll. G. C. Williams. SAM-H3409, 1 colony (Fig. 1E), off Danger Point, Cape Province, 34°40'S 19°17'E, depth 42 m, SCUBA, 13 April 1984, coll. W. R. Liltved.

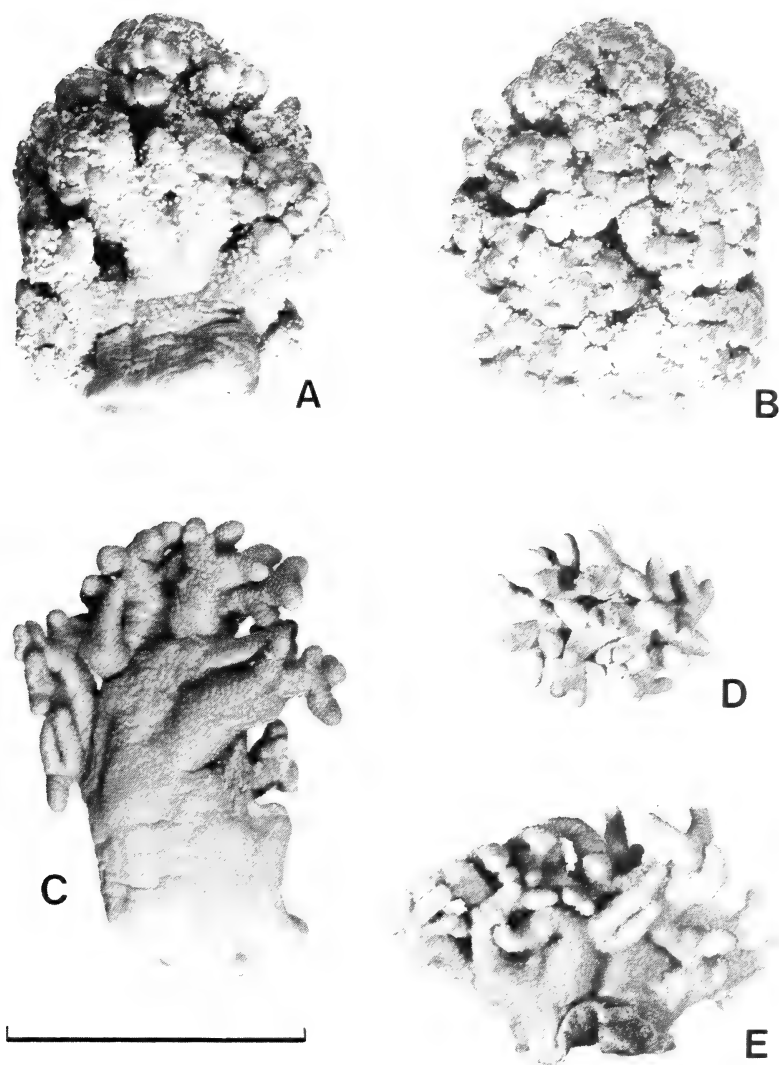


Fig. 1. *Alcyonium valdiviae* Kükenthal, 1906. A-B. SAM-H3347. C. SAM-H3732. D. SAM-H3384. E. SAM-H3409. Scale = 40 mm.

Description

External features (Figs 1A–E, 2A)

The colony (SAM–H3347) (Fig. 1A, B) measures 53 mm in total height, of which the stalk comprises 10 mm. The latter is laterally flattened and measures 22 mm at its greatest width. The polyparium is also slightly flattened. It consists of numerous closely set, round, sometimes rather conical, small lobes, 2–4 mm in diameter; these lobes are united into groups at the ends of twigs.

Many polyps are extended. Owing to their white colour they contrast distinctly with the dark-red colour of the polyparium. The anthocodiae protrude above the surface of the lobes for a distance of up to 0,20 mm (Fig. 2A). The tentacles are 0,40–0,50 mm long. At their bases they are swollen, about 0,13 mm wide, tapering distally to a sharp point. On either side they bear one row of 10–15 thin pinnules, 0,12–0,14 mm long. The polyps are entirely devoid of sclerites.

Sclerites (Figs 2C–D, 3A–I)

The rigid surface layer of the polyparium and stalk is densely packed with small capstans, which are primarily eight-radiates and six-radiates. The length of these sclerites is usually 0,05 mm and does not exceed 0,07 mm. There are also some four-radiates, as well as some three-radiates, 0,025–0,04 mm in length. The interior of the colony is devoid of sclerites.

Colour

The whole colony is orange-red, the polyps are white.

Variability

The five colonies differ in shape and in colour. The colony depicted in Figure 1C has a long, broad stalk. The specimens shown in Figure 1D–E have short stalks. The lobes may be short and conical, long and conical, or finger-shaped (Fig. 1C–E). The colony represented in Figure 1C is orange distally, but towards the base is light pink. The colony shown in Figure 1D is yellowish-grey; that in Figure 1E is pinkish-beige. The specimen from Gonubie (SAM–H3661—not illustrated) is bright yellow; this colony has a few extended polyps.

Distribution (Fig. 2E)

South coast of South Africa.

Remarks

It is unknown to the authors whether Kükenthal's type specimen is still kept in some museum or collection, so it could not be investigated.

Some of the specimens may superficially resemble members of the genus *Cladiella* but, for the following reasons, cannot be included in that genus: *Cladiella* species contain double heads (see Bayer *et al.* 1983, figs 159, 160)

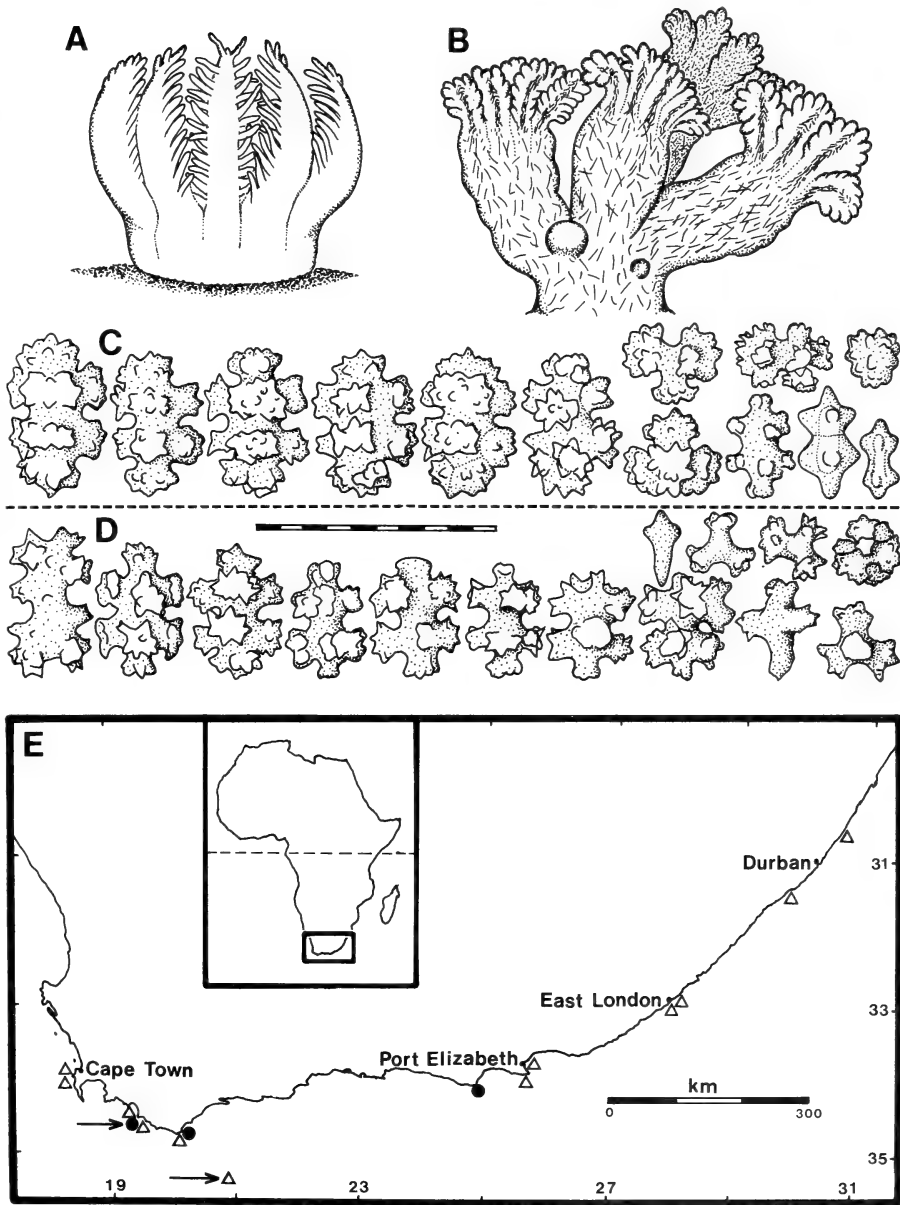


Fig. 2. A. *Alcyonium valdiviae* Kükenthal, 1906. A single polyp, 0,6 mm in height. B. *Litophyton liltvedi* sp. nov. A terminal lappet of four mature and two budding polyps, showing arrangement and relative density of sclerites in the polyp walls and tentacles. Total height of figure represents 3,3 mm. C-D. Sclerites of *Alcyonium valdiviae*. C. Sclerites from the surface of a lobe from the polyparium. D. Sclerites from the surface of the stalk. Total length of scale bar for C and D = 0,1 mm. E. Map of southern Africa showing collecting stations for *Alcyonium valdiviae* (Δ) and *Litophyton liltvedi* (\bullet). Arrows indicate type localities.

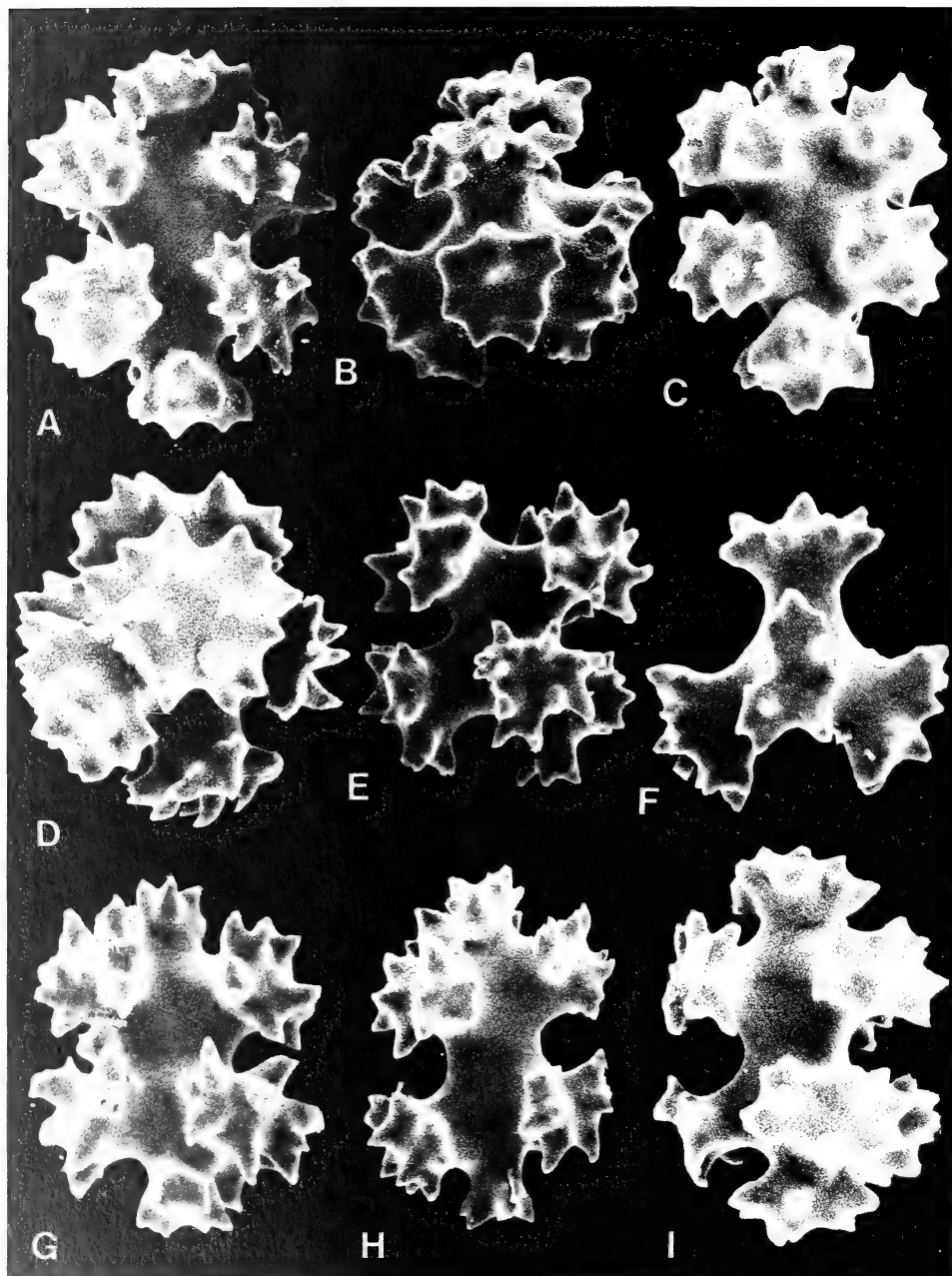


Fig. 3. *Alcyonium valdiviae* Kükenthal, 1906. Scanning electron micrographs of sclerites. A-D. Sclerites from the surface of a lobe from the polyparium. A. 0,053 mm. B. 0,042 mm. C. 0,053 mm. D. 0,048 mm. E-I. Sclerites from the surface of the stalk. E. 0,049 mm. F. 0,037 mm. G. 0,048 mm. H. 0,058 mm. I. 0,052 mm.

without terminal clusters of warts; the present specimens have capstans (see Bayer *et al.* 1983, figs 148–150). In all *Cladiella* species the interior contains sclerites; these are absent in the present specimens. *Cladiella* species have typical finger-biscuit-like sclerites in the surface layer of the lobes and/or in the polyps and/or in the tentacles; these are absent in the present specimens.

Hickson (1900) and J. Stuart Thomson (1910, 1921) referred the specimens examined by them to *Alcyonium pachyclados* Klunzinger, 1877 (a species that correctly belongs to the genus *Cladiella*). Although accurate in assigning the generic name *Alcyonium* to their material, they were incorrect as regards the specific identity for the above-stated reasons and since *Cladiella pachyclados* possesses coenenchymal sclerites that are much larger (up to 0,12 mm in length).

Alcyonium rutilum (Tixier-Durivault, 1954) from northern Natal closely resembles *A. valdiviae*. The two species can be differentiated as follows: *A. valdiviae* varies in colour from white to pink, yellow, orange, or orange-red, and possesses sclerites of capstans mostly 0,05–0,07 mm in length; *A. rutilum*, on the other hand, is deep wine-red or dark red and the sclerites (also capstans) do not exceed 0,04 mm in length. *Alcyonium rutilum* is known only from the holotype. Additional material is necessary to assess the extent of the intraspecific variation and to determine if it is truly distinct from *A. valdiviae*.

Family Nephtheidae Gray, 1862

Litophyton Forskål, 1775

Litophyton liltvedi sp. nov.

Figs 2B, E, 4–8

Material

SAM–H3393, holotype, off Danger Point, Cape Province, 34°38'S 19°20'E, depth 31 m, SCUBA, 10 April 1984, coll. W. R. Liltved.

Description

External features (Figs 2B, 4A–B)

The roughly circular, more or less flat, soft colony has diameters of 80 mm and 90 mm. On one side, where the excentrically situated stalk is found, the thickness of the colony is 35 mm; on the opposite side it is 10 mm thick. The holdfast is oval in shape, with diameters of 12–18 mm and 40 mm. (In Fig. 4B it is the dark patch at the lower side of the photograph.) From the stalk two stems arise: a short one, which passes into a small part of the polyparium, and a larger one, which is much branched and bears a larger part of the polyparium.

The upper side of the colony is covered with lobes. The larger ones are 10–15 mm wide. The extended polyps measure 1,60–2,50 mm in total height, the anthocodiae are 0,95–1,30 mm long (Fig. 2B). The extended tentacles, which are 0,60–0,70 mm long, have a single row of 5–7 pinnules on each side.

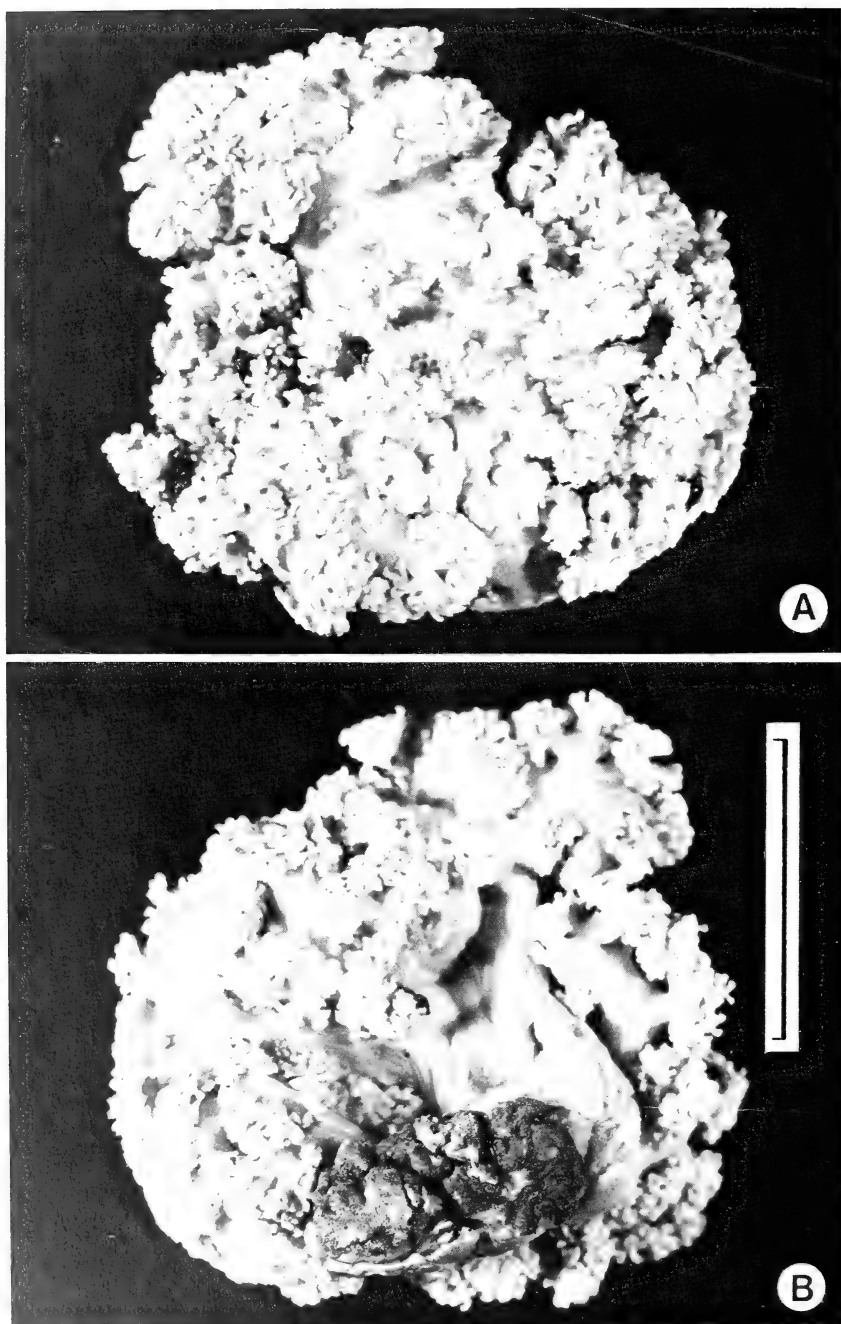


Fig. 4. *Litophyton liltvedi* sp. nov. SAM-H3393, holotype. A. Seen from above. B. Seen from below. Scale = 40 mm.

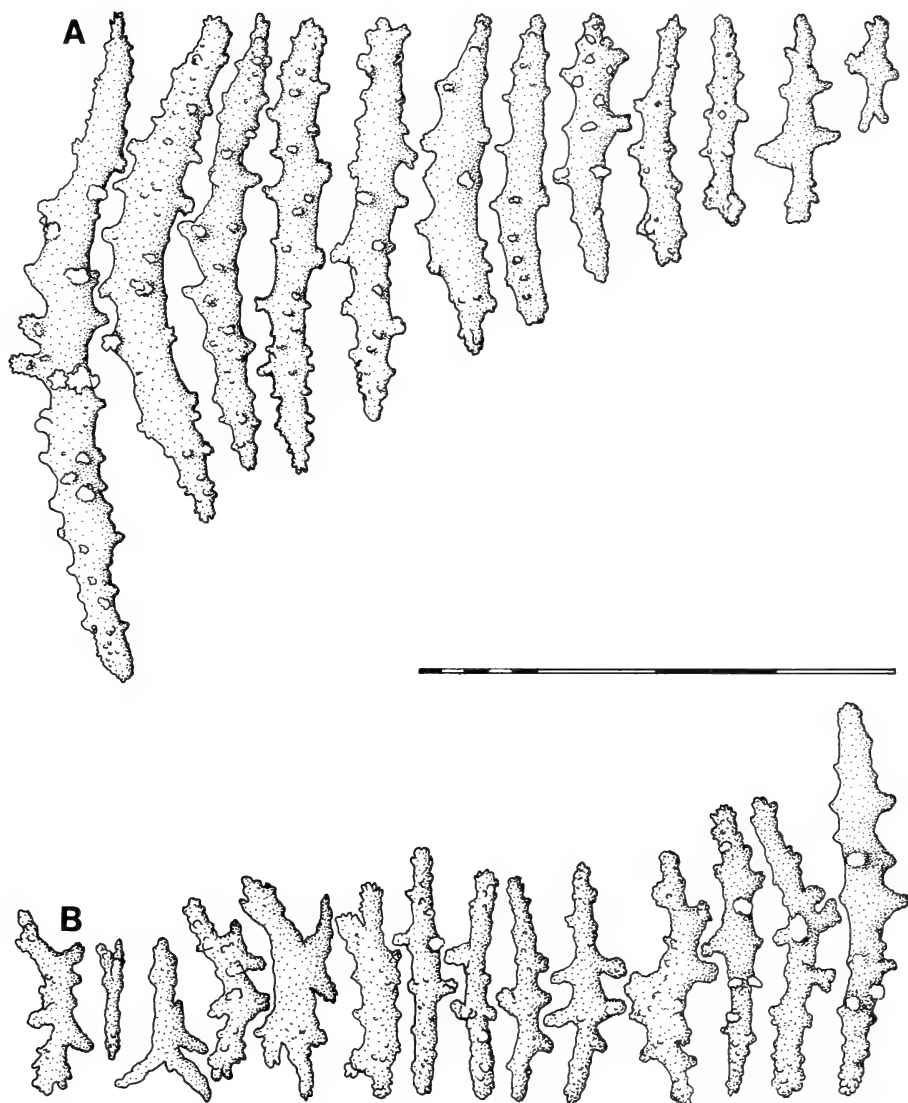


Fig. 5. *Litophyton liltvedi* sp. nov., holotype. A. Sclerites from the polyp wall. B. Sclerites from the tentacles. Entire scale bar represents 0,2 mm.

Sclerites (Figs 5–8)

The tentacles contain many spiny and wed spindles 0,05–0,16 mm in length (Figs 5B, 7A–F); in the base of the rachis the spindles are longitudinally arranged, while distally they are shorter and are arranged more or less *en chevron*.

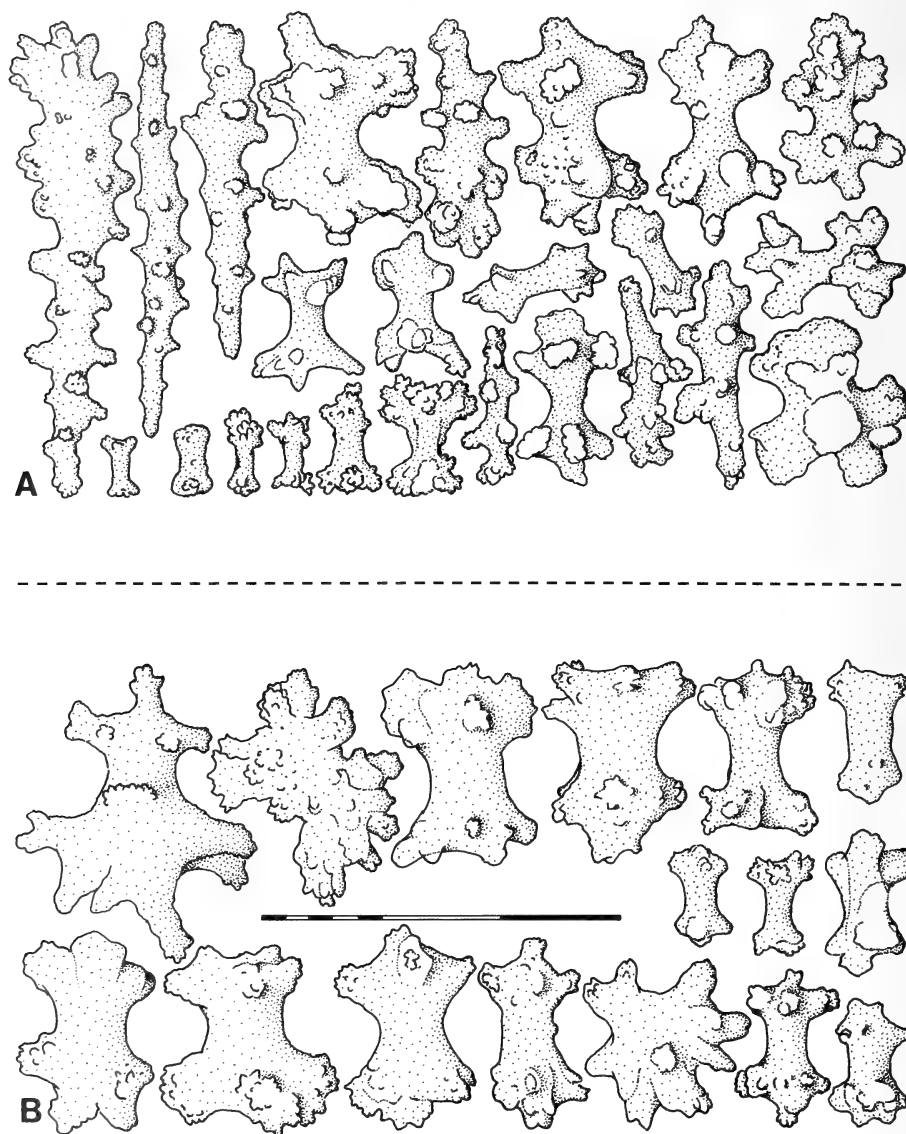


Fig. 6. *Litophyton liltvedi* sp. nov., holotype. A. Sclerites from the surface of a lobe from the polyparium. B. Sclerites from the surface of the stalk. Entire length of scale bar represents 0.15 mm.

The anthocodial wall contains spiny spindles (Figs 5A, 7G-L), usually more or less longitudinally placed, but they often lie crisscross, and thus do not present a typical crown-and-points arrangement (Fig. 2B). Proximally their length is 0.20-0.28 mm; towards the tentacles they are shorter, about 0.05-0.10 mm.

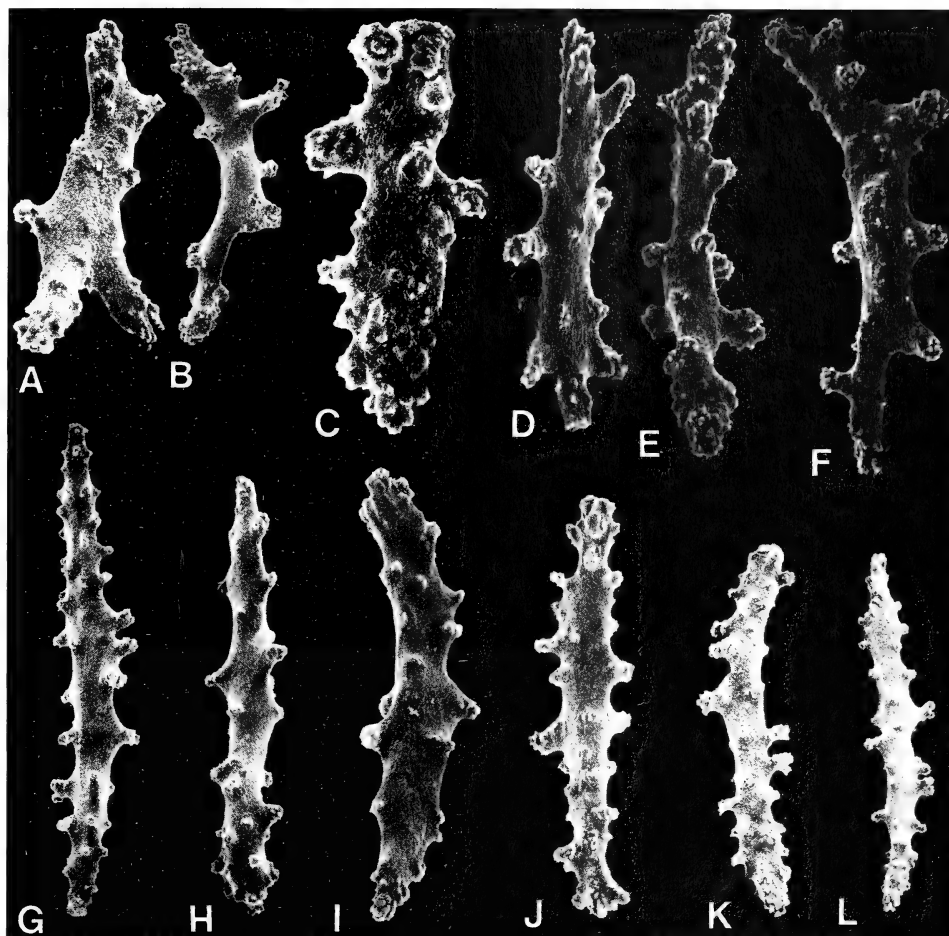
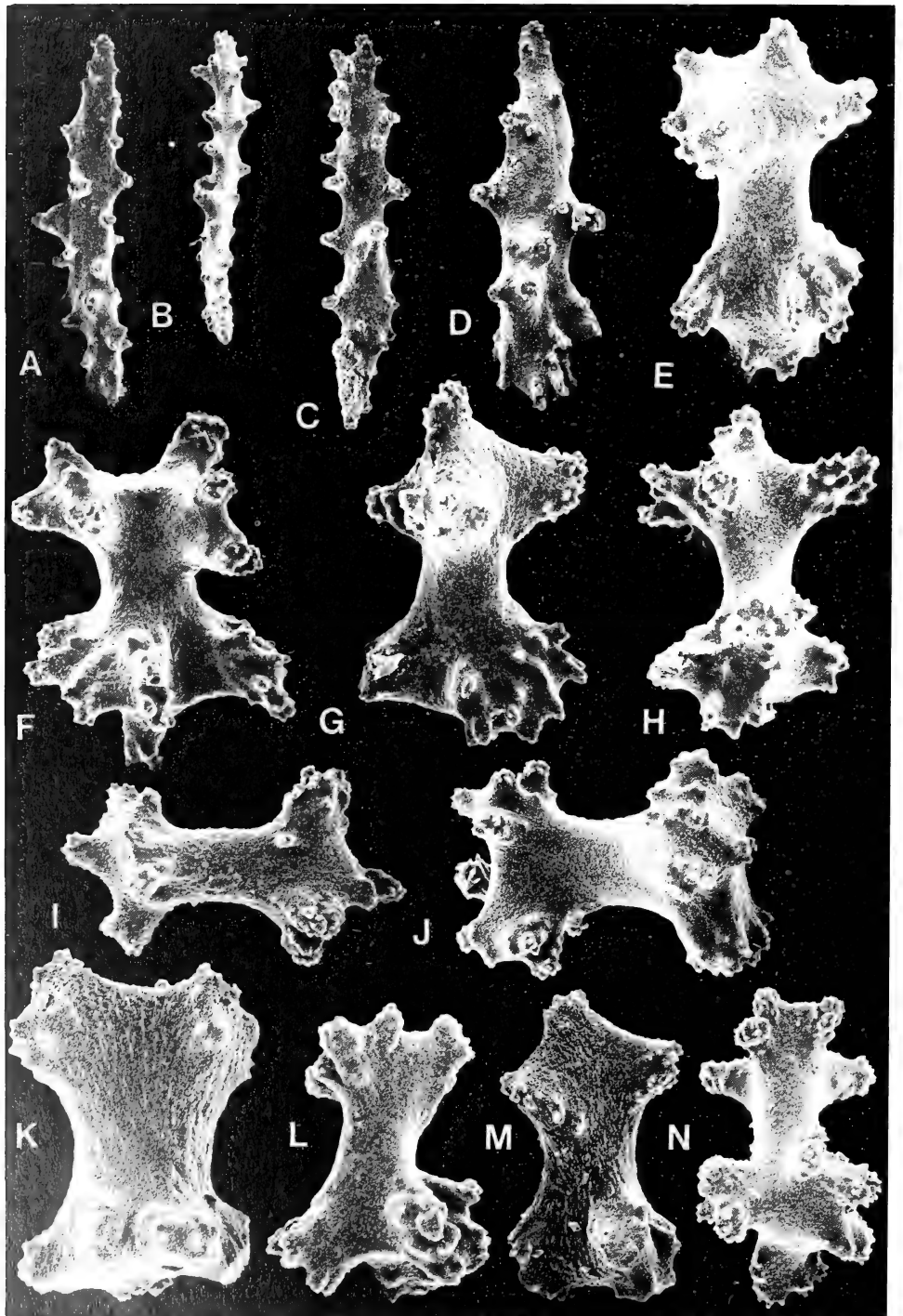


Fig. 7. *Litophyton liltvedi* sp. nov. Scanning electron micrographs of sclerites. A-F. Sclerites from the tentacles. A. 0,074 mm. B. 0,120 mm. C. 0,063 mm. D. 0,080 mm. E. 0,105 mm. F. 0,108 mm. G-L. Sclerites from the polyp wall. G. 0,212 mm. H. 0,163 mm. I. 0,150 mm. J. 0,150 mm. K. 0,155mm. L. 0,200 mm.

The surface layer of the polyparium and stalk contains many tiny double stars (usually 0,075 mm long, but ranging between 0,025 mm and 0,12 mm) with a proportionally long 'waist' (Figs 6A, B, 8E-N). In addition, in the surface layer of the terminal branches there are some spiny spindles, 0,08-0,20 mm long (Figs 6A, 8A-D). The two types of sclerites are not particularly densely set; in the interior of the colony sclerites are very scarce or absent.

Colour

In alcohol the colony is cream.



Etymology

Litophyton liltvedi is named for Mr W. R. Liltved, who collected the specimen on which this description is based.

Distribution (Fig. 2E)

South coast of South Africa.

Remarks

At first sight the colony resembles the type specimen of the alcyoniid *Alcyonium fauri*, as illustrated by J. Stuart Thomson (1910, pl. 1 (fig. 5)). However, in important respects the present specimen differs from the type of that species. According to Thomson the colony of *A. fauri* is encrusting, fairly hard, and the lobes are closely adjacent. The colony of *L. liltvedi* sp. nov. is not encrusting, and it is not hard but weak and flexible. The lobes do not arise from a lamella but rather from a fleshy polyparium, and the latter is provided with few rather than numerous spicules. Finally, in *A. fauri* the sclerites are up to 0,12 x 0,09 mm. Unfortunately, Thomson's figures of these sclerites (1910, pl. 4 (fig. 44)) are far from clear; with difficulty they can be discerned as double heads or dumb-bells with a very short waist. They are totally different from the double stars in *L. liltvedi* sp. nov. Examination of recently collected material referable to *A. fauri* has shown that a variety of coarsely tuberculated coenenchymal sclerites are evident, including robust spindles, wart clubs, double heads, and eight-radiates. Double stars are absent altogether.

The only other southern African soft coral that resembles *L. liltvedi* sp. nov. in its cauliflower-like appearance, is the nephtheid *Capnella thyrsoides* Verrill, 1865. The two are distinguished by the fact that the genus *Capnella* possesses many coenenchymal sclerites that are leaf clubs, whereas *Litophyton* is altogether lacking in leaf clubs.

The new species is referred to the genus *Litophyton* on the following grounds: (a) the colony branches repeatedly, and (b) the polyps are not retractile, they lack a supporting bundle, they are arranged in terminal catkins, and the anthocodial sclerites are not leaf clubs.

Small sclerites, but a little larger than the tiny double stars in the holotype, also occur in other *Litophyton* species, e.g. *L. stuhlmanni* (May, 1899) and *L. confertum* Kükenthal, 1903.

Fig. 8. *Litophyton liltvedi* sp. nov. Scanning electron micrographs of sclerites. A-H. Sclerites from the surface of a lobe from the polyparium. A. 0,210 mm. B. 0,155 mm. C. 0,180 mm. D. 0,125 mm. E. 0,085 mm. F. 0,090 mm. G. 0,083 mm. H. 0,075 mm. I-N. Sclerites from the surface of the stalk. I. 0,090 mm. J. 0,075 mm. K. 0,078 mm. L. 0,065 mm. M. 0,090 mm. N. 0,090 mm.

ACKNOWLEDGEMENTS

I thank Dr G. C. Williams, Department of Marine Biology, South African Museum, Cape Town, for the loan of the material; he also put me on the track of *Alcyonium valdiviae*. As always I am indebted to my friends Mr G. J. Vrijmoeth, for taking the photographs of the corals, and Mr W. ter Spill, for reading the text (J.V.).

I am grateful to Klaus Schultes and Dane Gerneke of the Electron Microscope Unit, University of Cape Town, for technical assistance with the preparation of scanning electron micrographs; Michelle van der Merwe and Elizabeth Hoenson, South African Museum, for assistance with the preparation of Figures 3, 7 and 8, and for curatorial work; and Elizabeth Louw, Editor, South African Museum, for comments and suggestions (G.C.W.).

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers.

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text

e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names

e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives

e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should preferably be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

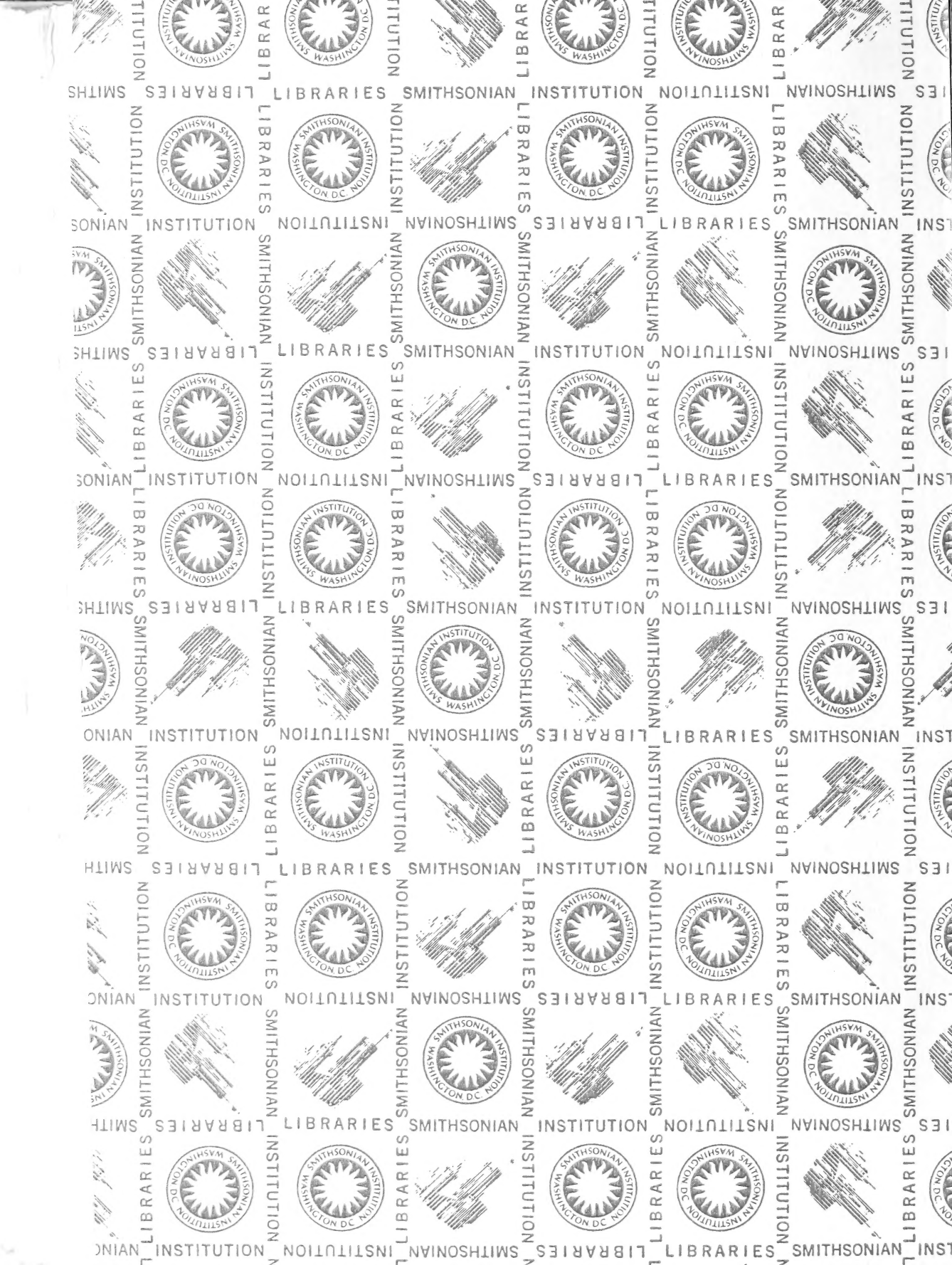
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

J. VERSEVELDT & GARY C. WILLIAMS

A REDESCRIPTION OF THE SOFT CORAL
ALCYONIUM VALDIVIAE KÜKENTHAL, 1906, WITH
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LITOPHYTON FORSKÅL, 1775, FROM SOUTHERN
AFRICA (OCTOCORALLIA, ALCYONACEA)





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